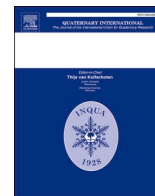




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## Insects and molluscs of the Late Pleistocene at the Gornovo site (Southern Ural foreland, Russia): New data on palaeoenvironment reconstructions

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### ABSTRACT

The paper presents new data on the subfossil insects and molluscs, as well a new radiocarbon date for the Gornovo site in the Southern Fore-Urals. As a result, the stratigraphic interpretation of the sediments of the lower part of the first above floodplain terrace of the Belaya River is corrected and they are assigned to the Tabulda Horizon (MIS 3) of the Upper Pleistocene in the regional scheme of the Fore-Urals Quaternary. The malacofauna of the locality is represented by 27 species of terrestrial and freshwater molluscs. The composition of molluscs in the deposits of MIS 3 indicates the succession of deposit accumulation in the river valley from the stage of reservoirs that periodically connecting with the river to the stage of the overgrown oxbow lake. Single occurrence of mollusc shells in the loams of MIS 2 is a result of sharp climate change. New insect material includes 136 species of Coleoptera from 17 families, as well as Heteroptera and Hymenoptera representatives. 29 species of beetles (Carabidae, Histeridae, Scarabaeidae, Elateridae, Tenebrionidae, Chrysomelidae, Brentidae and Curculionidae) are recorded for the Pleistocene for the first time. The insect assemblages from Gornovo site are assigned to periglacial and humid boreal faunal types. The entomofauna of the periglacial type has no analogues in the recent fauna; it corresponds to the deposits assigned to the middle of MIS 3. This entomofauna is characteristic to the MIS 2 and MIS 3 insect assemblages from the south of West Siberian Plain. Based on entomological data, the climate of the middle of MIS 3 of the Southern Fore-Urals is reconstructed as dry and cold, extracontinental, with mean July temperature not exceeding +15 °C. Steppe landscapes likely prevailed in open areas and coniferous forests were restricted to river valleys. Beetles from deposits dated to end of MIS 3 are assigned to the fauna of the boreal humid type. These insect assemblages are significantly poorer in diversity than periglacial type assemblages and are represented mainly by near water and forest Coleoptera. Based on these species, meadow and forest landscapes were reconstructed. The reconstructed mean air temperature of July ranged from +16 to +19 °C. This suggests a trend towards more mild conditions in the region connected to the climate warming at the end of MIS 3. It is likely that humidification during this period was regional, determined by the proximity of the site to the Southern Urals Mountains.

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## 1. Introduction

Quaternary insects have been studied for over 60 years. They are used by palaeoecologists as a proxy for reconstructing the environment along with other groups of fossils (Kuzmina, 2017). However, the degree of knowledge of subfossil insects remains very uneven, especially geographically. Subfossil insects from Europe have been studied extensively (BugsCEP database; Buckland, 2014). In Russia, Early Pleistocene – Late Holocene insects are known from localities in Yakutia and Chukotka (Kuzmina and Matthews, 2012; Kuzmina, 2015). They are also known from the West Siberian Plain and the Urals (Zinovyev, 2008, 2011; Zinovyev et al., 2016; Gurina et al., 2018, 2019a, b). Finally, some information is available about Quaternary insects in the Northern Caspian region (Bidashko and Proskurin, 1984, 1987; Bidashko, 1994).

Most of the vast territory of Russia has not been represented in studies of Quaternary insects. One notable deficiency is the Southern Urals foreland, from which the only Gornovo site is known. Quaternary insects were discovered there by Bidashko in 2003, but, unfortunately, no results of this study have been published. Later, a team of researchers (Danukalova et al., 2016) made a summary of biostratigraphic data from the Gornovo site. A complex of insects was identified and compared with the interstadial MIS 3. This complex consisted of inhabitants of the forest-steppe and forest zones and near-water biotopes. Similar ecological complexes were also discovered based on macro-fossil remains of plants, ostracods, and molluscs, which suggested palaeoreconstructions similar to those based on insects. On the contrary, a steppe group is distinguished amongst mammals of the Tabulda time of the Gornovo site, including such notable species as the camel (Danukalova et al., 2016). The composition of the identified insect assemblage of Gornovo does not completely correlate with entomofaunas of a similar age in the adjacent territories of the West Siberian Plain, which are characterized

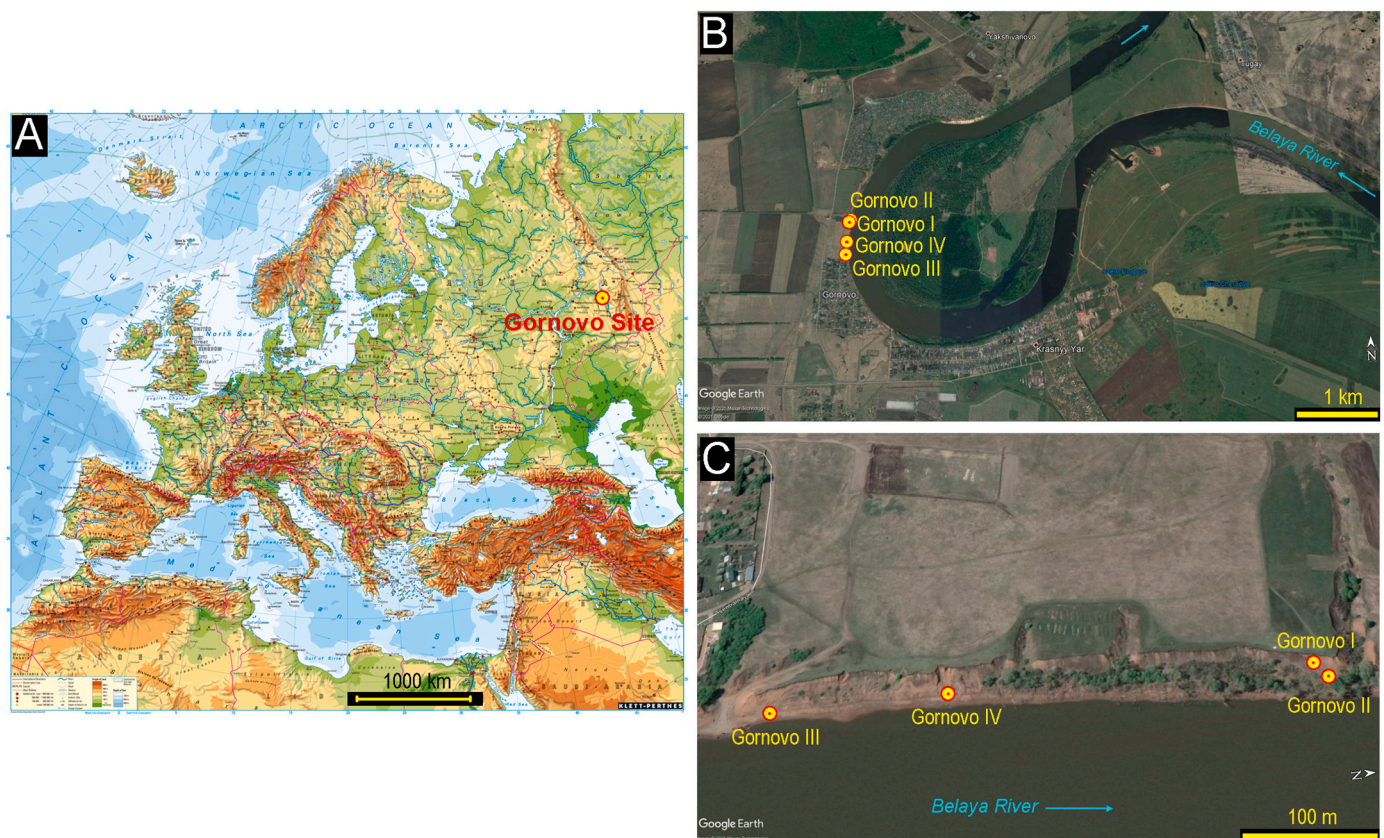
by species not present there in the recent fauna (Zinovyev, 2003, 2011; Gurina et al., 2018, 2019a). The West Siberian subfossil entomocomplexes are characterized by a combination of steppe and tundra groups.

To eliminate contradictions and establish a clear record of the entomofauna that inhabited Southern Urals foreland during Late Pleistocene, we carried out a new study of the deposits of the Gornovo site. Extensive entomological material obtained from this site forms the basis of this paper. In addition to insects, new materials on molluscs have also been obtained, which make it possible to test earlier results based on this group. In addition, by describing the stratigraphy of the new section and obtaining radiocarbon dating, we detected contradictions with the previous interpretation of the age of these deposits.

Thus, the main aim of this paper is to describe the entomofauna of Gornovo site and compare it with other Late Pleistocene faunas of adjacent regions, as well as to reconstruct the environment.

## 2. Regional setting – Gornovo site

The Gornovo site (54°54'27.30"N, 55°52'48.26"E) is located on the left bank of the Belaya River in the vicinity of the Gornovo village (Ufa District, Bashkortostan Republic) (Fig. 1). It is known primarily as an archaeological site with Late Palaeolithic tools. In 1959, Shokurov explored a horizon with an ancient fauna of large-mammal remains and discovered two flint tools (Shokurov and Bader, 1960). Later, this site attracted the attention of archaeologists, palaeontologists, and stratigraphers (Yakhemovich, 1965; Sherbakova, 1984; Khabibullina, 1986; Yakhemovich et al., 1987; Popova-Lvova, 1988; Danukalova et al., 2000, 2002). Recently Danukalova et al. (2016) carried out a comprehensive study and summarized biostratigraphic data of the Gornovo site. For this purpose, three tranches were excavated and described, which made it possible to identify deposits of different ages and to analyse



**Fig. 1.** (A) The study area within the map of Europe (a map is based on the preview-map of KLETT-PERTHES, <https://www.worldmaponline.com/klett-perthes/>). (B, C) The images of the studied area showing the Gornovo I, II, III and IV sections (the images are based on data of the Google Earth). Direction of the river flow is indicated by a blue arrow. (For interpretation of the reference to colour in this figure legend, the reader is referred to the Web version of this article).



significant palaeontological material including: spore and pollen, macro-remains of plants, ostracods, molluscs, small and large mammals, and insects. All deposits are correlated to the regional stratigraphic scheme of the Fore-Urals Quaternary deposits given in Danukalova (2010) (Table 1).

The Gornovo site is attributed to the first level above a floodplain terrace. A term 'river terrace' represents a former level of the river valley (floodplain); a terrace results from any hydrological/climatic/tectonic shift that causes renewed downcutting (Britannica, 2021). Usually the bulk of the available information about fluvial deposits is coming from geomorphology, by recognizing river terraces and correlating them by their height above river level. As it was indicated by Matoshko et al. (2004) this approach has been improved (for example, Obedientova, 1977) but, for it to be a reliable technique, an accompanying geological investigation is required. Its application in isolation is probably a key reason for the great divergence of opinions on the nomenclature, age and occurrence of the river terraces within each valley. Many terraces are formed by several superimposed alluvial suites and their sections include non-fluvial deposits. There can be several terraces above the floodplain in the river valley. Terraces are counted from below, from younger to older ones. The first terrace above the floodplain rises above the floodplain, the second is higher, etc. The relative height of the terraces is measured from the low-water level of the river. The highest terrace is the oldest, the lowest is the youngest. In case of the river valleys of the Fore-Urals and Urals affected by the accelerating uplift of the territory (Puchkov and Danukalova, 2009), there is a flood plain of lower and of higher levels; the high floodplain level can be considered as a terrace, but alluvial deposits forming it accumulated during Early-Middle Holocene and not the Pleistocene. However, during very high floods, these high floodplains can be covered by water. In this study the authors use a term 'above floodplain terrace' to mean that the main alluvial body is located above the flood plain of the river valley and the deposits, which form it, are older than the Holocene; at the same time, a soil at the top of the terrace was formed during Holocene (Yakovlev et al., 2013; Danukalova et al., 2014).

All river terraces are numbered starting from the flood plain level. The age of the sediments, occurring in the lower part of the terrace, was established on the indirect data. The crossbedded lamination and sandy facies suggest that lower part of these deposits was accumulated under the influence of a river current (Belaya Horizon); the alternation of sands and clays overlaying sands suggest the conditions with periodical shifts of the river current from riverine to stagnant (limnic) environments (Larevka Horizon). The bones of large mammals found on the surface of the sands belong to the Khazar Middle Pleistocene faunistic complex. It was assumed that the bones were washed out of the sands of the lower part of the section; therefore, the sands were attributed to Belaya Horizon (Yakhemovich et al., 1987) (Table 1). Yakhemovich et al. (1970) described alluvial deposits of the Belaya Horizon as deposits forming the ancient riverbed of the Belaya River.

The lower part of the sediment succession presented by alluvial and lacustrine deposits which overlay sands, have traces of frost penetration (Gornovo II, layer 5) (Yakhemovich et al., 1987). These deposits also contain palaeocarpological remains (Gornovo III, layer 4) determined by Dorofeev, who stated the existence of glacial forms and similarity of this flora to the Eastern European glacial floras. Dorofeev concluded that the flora from the Gornovo sections is of pre-Saalian/Khazar age (Yakhemovich et al., 1987; Danukalova et al., 2016). Therefore, these deposits were also correlated to Middle Pleistocene but to cold Larevka Horizon.

The deposits forming the upper part of the terrace (regional Tabulda and Kudashevo Horizons, Upper Pleistocene) are well correlated with the geochronological scale. The deposits attributed to Tabulda Horizon were characterized best of all other deposits – numerous fossil remains and artefacts were found there. The age of the deposits is reliably correlated with the geochronological scale based on a series of radiocarbon dates (Danukalova et al., 2016). Artefacts found *in situ*, are characteristic for localities that date to the beginning of the Upper

Palaeolithic, a period that correlates to the last optimum of the Middle Valdai (32–24 ka) (Velichko and Ivanova, 1969; Rogachev and Anikovich, 1984; Sherbakova, 1984; Yakhemovich et al., 1987). Data on molluscs and ostracods suggest existence of an oxbow lake with periodical connection with the river at times of floodings. Forests grew on the banks of the river; open landscapes covered interfluvies. Bones of large mammals belong to the early stage of the Late Palaeolithic complex (Yakhemovich et al., 1987). The small mammal fauna (Danukalova et al., 2016) can be correlated with the Late Pleistocene stage of the small-mammal fauna development of Eastern Europe (Agadjanian, 2009). Beetle species could inhabit intrazonal biotopes with well-developed dense riparian vegetation, and protected species which inhabited the interfluvie biotopes. The presence of a few beetle species that preferred forest biotopes suggests the existence of floodplain forests. The palaeoclimate was somewhat cooler than recent conditions of the Southern Fore-Uralian area (Danukalova et al., 2016). Spore and pollen data reconstruct forest-steppe landscapes that dominated during the Tabulda Interstadial (MIS 3) (Danukalova et al., 2016).

The Kudashevo Horizon sediments overlie the dated Tabulda clays; respectively; they are younger than  $25570 \pm 790$  cal BP. These sediments form the upper part of the first above-floodplain terraces in the region and they are represented by light brown loess-like loam with columnar jointing. The grassland-steppe association covered most part of the territory during the Kudashevo time. A *Picea* forest with leaved trees admixture grew in moist depressions. The climate was cold. Data on the molluscs suggests the habitat corresponded with a cool steppe-like or forest-steppe environment (Danukalova et al., 2016).

The stratigraphical position of the studied deposits of Gornovo and the correlation between the Middle and Upper Pleistocene deposits of the Gornovo I–III sections and newly studied Gornovo IV section are presented in Fig. 2.

### 3. Material and methods

We used palaeontomological as the main method. Data on molluscs were analysed for supporting evidence from an additional group.

#### 3.1. Sampling

To obtain new materials on the Quaternary insects of the Gornovo site, a field expedition was carried out in 2018. The Gornovo II section, from which entomological data were obtained earlier (Danukalova et al., 2016), has become unavailable for study because the landslides have covered the terrace slope. Therefore, approximately 340 m upstream from Gornovo II along the Belaya River, a new Gornovo IV section was carried out and layers containing fossil remains were found (Figs. 1C, 2).

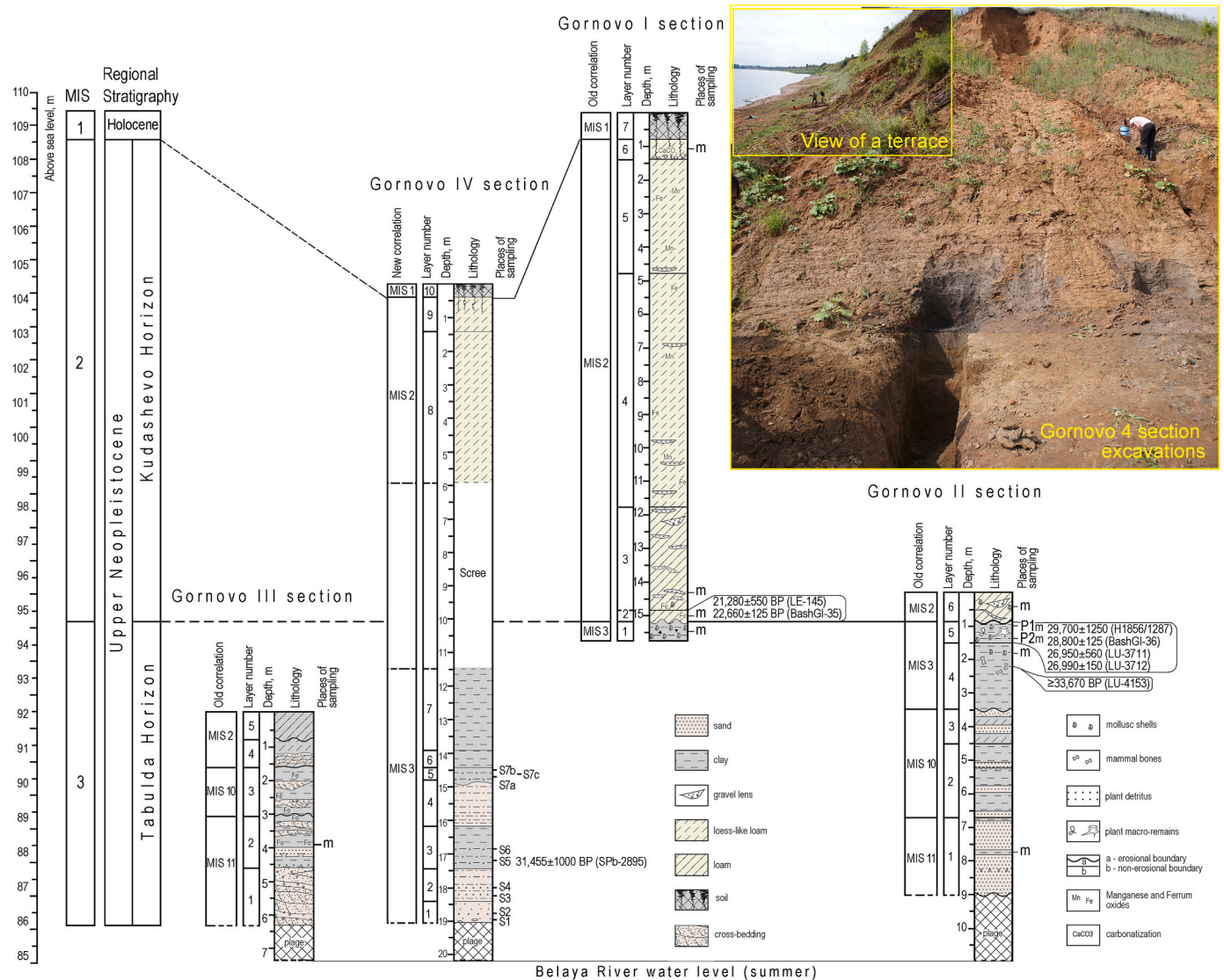
Insect samples were taken using standard techniques (Coope, 1959; Kuzmina, 2017; Gurina et al., 2019b), with some modifications and additions. After sectioning, the samples were taken within each layer (Supplementary Table 1), each in several replicates (sub-samples). The volume and number of samples were determined based on the concentration of insect fragments in the sediments in order to obtain a representative material (about a hundred or more fragments). In case of a low concentration of plant residues and insect fragments in the sediments, the samples were enriched (samples S3–S7). For this, the sediments were subjected to wet sieving in filtered river water through a sieve with a mesh diameter of 0.3 mm. The resulting concentrate was placed in plastic bags for further processing in the laboratory. With a high concentration of plant residues, the entire piece of deposit was placed in plastic bags (samples S1 and S2).

In the Gornovo IV section, seven samples were taken for entomological analysis (Supplementary Table 1). Three samples for malacological analysis were taken from the layer 5 simultaneously with samples for entomological analysis using the same technique (Table 2).

**Table 1**  
Correlation between the Middle and Upper Pleistocene subdivisions of the Fore-Urals, Western Europe and the Central European part of Russia.

Global Quaternary scheme (Cohen and Gibbard, 2019)			Marine Isotope Stages Lisiecki and Raymo (2005)	General Stratigraphic Scheme of Russia (Zhamoïda et al., 2019)		Southern Fore-Urals (Danukalova, 2010)			European part of Russia Shik (2014)			West European stratigraphic divisions (The Netherlands)/ Ma (Turner, 1998; Zagwijn, 1996)	
System	Series	Subseries, stages		Division	Member, Lower boundary age, Ma	Superhorizon	Horizon	Subhorizon	Superhorizon	Horizon	Subhorizon		
QUATERNARY	HOLOCENE	LATE	1	Holocene	Upper		Agidel	Upper		Shuvalovo	Upper	Upper	
		MIDDLE			Middle			Middle			Middle	Middle	
	PLEISTOCENE	EARLY	2	NEOPLEISTOCENE	Lower (0.0117)	Valdai	Kudashevo	Lower	Valdai	Ostashkov	Lower	Upper Weichselian	
		LATE	3		Upper (0.126)		Tabulda			Leningrad		Middle Weichselian	
			4				Saigatka			Kalinin		Lower Weichselian	
			5a-d				Kushnarenkovo			Chermenino			
			5e			Middle Russian			Middle Russian	Mikulino		Eemian	
		MIDDLE	6		Middle (0.427)		Elovka			Moscow		Saalian	Drenthe glaciation
													Cold Interval with permafrost
			7				Klimovka			Gorky		Bantega	interstadial
			8							Vologda			Cold Interval
			9							Chekalin			Hoogeveen
													Interstadial
			10				Larevka			Kaluga			Cold interval with permafrost
			11				Belaya			Likhvin			Holsteinian Interglacial
			12		Lower		Chusovskoi			Oka			Elsterian





**Fig. 2.** The correlation between the Gornovo I-III sections, recently studied Gornovo IV section, a plan with the location of the sections, and a scheme of river valley with geomorphological elements. Holocene is represented by Agidel Horizon in the Regional Scheme of Fore-Urals area.

### 3.2. Entomological methods

In the laboratory, the resulting concentrate (or original deposit) was washed with tap water and separated into fractions using sieves with a mesh diameter of 2 mm, 0.6 mm, and 0.3 mm. The fractions were dried at room temperature. After drying, the remaining insect fragments were picked up under a binocular microscope. Then the fragments were sorted into “potentially identifiable” and “not suitable for determination”. “Potentially identifiable” fragments (whole or halves of head capsules, elytra, pronotum, puparia, terminalia, etc.) were washed with the Sanelit detergent, then in a stream of water from a syringe and afterwards glued to cardboard plates with water-soluble glue. Each fragment was labelled and entered into the database. Except the sub-samples S3 and S7 which were processed completely, only a part of the sub-samples taken was processed, since a sufficient number of fragments were obtained from them for analysis already (Supplementary Table 1).

The identification of the species was carried out by comparing fragments with recent material. For comparison, the collections of the following institutions were used: Institute of Systematics and Ecology of Animals Siberian Branch of RAS (Novosibirsk), Institute of Plant and Animal Ecology, Ural Branch of RAS (Ekaterinburg), Zoological Institute of RAS (St. Petersburg), Paleontological Institute of RAS (Moscow),

Zoological Museum of Moscow M.V. Lomonosov State University, Moscow M.V. Lomonosov State University, and Moscow Pedagogical State University.

To estimate the number of individuals of each species in the samples, the minimum number of individuals’ indicator ( $N_{min}$ ) was used. Since the exoskeleton of insects disintegrates into parts during burial, the actual number of individuals may be less or equal to the number of fragments. At the same time,  $N_{min}$  was calculated based on the assumption that those parts of the exoskeleton that could belong to one insect actually belonged to it. Numerically, for each beetle species, it equals to the maximum number of fragments of one type (head, pronotum, left or right elytron).

When comparing the species composition, the Szymkiewicz-Simpson pairwise similarity coefficient ( $K_s$ ) was used:  $K_s = c / \min(a, b) \times 100\%$ ; where  $a$  and  $b$  are the numbers of species in the first and second samples, respectively, and  $c$  is the number of common species in these samples (Pesenko, 1982; Magurran, 2004).

The Mutual Climatic Range (MCR) method was used to reconstruct the average temperature of the warmest month, July ( $T_{max}$ ) (Coope, 1977; Alfimov et al., 2003; Bray et al., 2006). To determine the temperature limits  $T_{max}$ , the most thermophilic, on the one hand, and cold-loving species on the other hand, were mapped for each sample.

**Table 2**

The stratigraphical distribution of the molluscs in the Gornovo site including new data on the Gornovo IV section.

N	Species Horizon	Tabulda						Kudashevo					
		Section	II	III	IV	IV	IV	II	II	I	II	I	I
		Layer	6	4	5/ S7a	5/ S7b	5/ S7c	3	2	7	1	6	5
1.	<i>Succinella oblonga</i> (Draparnaud, 1801)		1	11	128	270	192	100	100	100	4	9	83
2.	<i>Succinea cf. putris</i> (Linnaeus, 1758)						1						
3.	<i>Oxyloma elegans</i> (Risso, 1826)					1		140	100	100			
4.	<i>Pupilla muscorum</i> (Linnaeus, 1778)			1	3	3	34	100	50	50		7	
5.	<i>Vallonia tenuilabris</i> (Al. Braun, 1842)		5	2	2	10	15	94	100	100		1	30
6.	<i>Vallonia pulchella</i> (Müller, 1774)						1						
7.	<i>Discus rudieratus</i> (Ferussac, 1821)							1					
8.	<i>Pseudotrichia rubiginosa</i> (Rossmässler, 1838)							24	2	2	2		1
9.	<i>Lymnaea palustris</i> (Müller, 1774)			3	28	407	113	200	5	5			
10.	<i>Anisus spirorbis</i> (Linnaeus, 1758)			8		76	95	243	58	100		1	
11.	<i>Anisus vortex</i> (Linnaeus, 1758)						1						
12.	<i>Planorbis planorbis</i> (Linnaeus, 1758)			4				12	2	2			
13.	<i>Gyraulus laevis</i> (Alder, 1838)		1	8	174	1138	364	300	500	50			
14.	<i>Bathyomphalus contortus</i> (Linnaeus, 1758)							2	1	1			
15.	<i>Aplexa hypnorum</i> (Linnaeus, 1758)				1	18	2						
16.	<i>Valvata pulchella</i> Studer, 1820			4			1						
17.	<i>Valvata antiqua</i> Sowerby, 1852							1					
18.	<i>Valvata</i> sp.				1	2							
19.	<i>Bithynia</i> sp.							1					
20.	operculum <i>Bithynia</i> cf. <i>trochellii</i> Paasch, 1842							2	4				
21.	operculum <i>Bithynia</i> cf. <i>tentaculata</i> (Linnaeus, 1758)					1			1				
22.	<i>Viviparus</i> sp.			9									
23.	<i>Sphaerium rivicola</i> (Lamarck, 1818)			16				1					
24.	<i>S. corneum</i> (Linnaeus, 1758)			1									
25.	<i>Pisidium amnicum</i> (Müller, 1774)		2	9				1	1	1			
26.	<i>P. supinum</i> Schmidt, 1861			9									
27.	<i>Pyrgula</i> cf. <i>trivialis</i> Log. et Star., 1968												5
28.	<i>Clessiniola</i> sp.												1
29.	<i>Dreissena polymorpha</i> (Pallas, 1771)											11	
	Total number of remnants		9	85	337	1926	819	1122	924	511	6	9	85
	Palaeoenvironment		Riverine area	Riverine area	3082	Floodplain flooded during high water		Oxbow-lake	Overgrown oxbow-lake with spruces along the banks		Oxbow filled with sediments		River terrace

$T_{max}$  for each locality was estimated by extrapolating data from meteorological stations closest to the collection sites of these species. Average  $T_{max}$  by weather stations are available on the websites: [average-weather.com](http://average-weather.com), [pogodaiklimat.ru](http://pogodaiklimat.ru), [climate-data.org](http://climate-data.org). For widely ranged species the published temperature limits  $T_{max}$  was used (Elias, 2000; Buckland, 2014).

A total of 943 insect fragments were obtained from samples S1–S7 of the Gornovo IV section. The concentration of residues and the number of recovered fragments in the sediments varied significantly (Supplementary Table 1). The previously published P1 and P2 samples from the Gornovo II section (Danukalova et al., 2016) were also revised in comparison with the new material.

### 3.3. Malacological method

5892 complete shells including 3082 shells from newly studied Gornovo IV section represented the mollusc remains. The quantity of extracted shells varied per sample (Table 2). Their abundance is given according to the method of Ložek (1964). The number of complete shells plus the number of apices or apertures, which were considered as equivalent to one shell when taken together, were counted. Then, the resulting number of individuals assembled from matching fragments was added to the number of intact specimens.

Species determination was done following Zhadin (1952), Logvinenko and Starobogatov (1968), Likharev and Rammelmeier (1952), Shileyko (1984), Shileyko and Likharev (1986), Kerney and Cameron (1999), Nederlandse Fauna 2 (1998), Glöer (2002), Sanko (2007),

Sysoev and Shileyko (2009), Khokhutkin et al. (2009). For the malacological taxonomical nomenclature, we used the publication of Falkner et al. (2002).

Previously published data on the malacological samples from Gornovo I–III sections (Danukalova et al., 2016) have also been revised against new material.

### 3.4. Radiocarbon dating

We use the general stratigraphic divisions of the Russian stratigraphic scale (Zhamoida et al., 2019). Local stratigraphic subdivisions for the Southern Urals are given according to Danukalova (2007, 2010) as well as the stratigraphic scheme of the Middle – Upper Pleistocene of the Southern Fore-Urals and correlation with other regions (Table 1).

Radiocarbon dating was carried out based on the 100 g of plant detritus of the S5 sample in Herzen State Pedagogical University of Russia, St. Petersburg. The sample was purified by sequential treatment in hot solutions of hydrochloric acid (3%) and sodium hydroxide (1%). The cleaned sample was charred at 600 °C without oxygen and sintered with lithium. The resulting lithium carbide was hydrolysed, and benzene was synthesized from the released acetylene on a chromium catalyst. The benzene used as a counting agent after purification with sulphuric acid, sublimation, and addition of POPOP and POP scintillators. Radiocarbon activity was measured with a Quantulus 1220 scintillation counter (Kulkova, 2011). The obtained radiocarbon date is 31455 ± 1000 BP (SPb-2895). Calibration was performed using Calib Rev 8.1.0 software by curve IntCal20, range ±  $\sigma$ . The resulting calibrated age is

34723–36809 cal BP. In addition, previously published dates from the Gornovo site (Danukalova et al., 2016) were used in this work.

## 4. Results

### 4.1. Stratigraphy and chronology

During the field survey in 2018, the sediments that formed the first above floodplain terrace were excavated. The new excavation was located between the Gornovo III and I sections in the place with the least landslides on the slope. It was not possible to clear completely the middle part of the slope because of the water cut and voluminous landslide masses that covered the terrace slope. The description of the general geological section is as follows (from base to top starting from the Belaya River water edge on 6.08.2018 and riverbeach covered by grass and springs (thickness is 0.85 m)) (Fig. 2): Layer 1. Brown-grey, clayey polymictic sand with pebbles in the lower part of the layer and with two interlayers of dark brown plant remnants (the thickness of the interlayers is up to 1–4 cm) (samples S1, S2), located 0.25 m from the bottom of the excavation; mollusc shells detritus present in the interlayers (excavated thickness is 0.65 m). Layer 2. Brown sandy loam with two interlayers (thickness of interlayers – up to 10 cm) of dark grey viscous clays with plant remnants (samples S3 and S4); above – sandy loam with interlayers of dark grey clays (thickness is 0.57 m) is located above sandy loam (thickness is 0.92 m). Layer 3. Dark grey clay, viscous, thin subhorizontal or wavy-layered with black plant remains (samples S5, S6). Above, dark grey clay gradually turns into brownish-grey clay (thickness is 0.32 m). Water oozes at the upper boundary of the layer (thickness is 1.24 m). Layer 4. Brown sandy loam, thin subhorizontal-wavy with interlayers of brown dense clay (thickness of interlayers is up to 2 cm). The clay of layer 4 gradually transforms into clays of layer 5 (thickness is 1.4 m). Layer 5. Dark grey to black clay with plant remnants (sample S7), mollusc shells. Erosion and ferruginization are observed along the lower boundary of the layer (thickness is 0.35 m). Layer 6. Brownish-grey dense, viscous clay (thickness is 0.45 m) Layer 7. The clay is greyish-brown, viscous, and less dense than the clay in layer 6 (excavated thickness is 2.4 m) Landslide and talus (5.6 m thick). Layer 8. Light brown-greyish loam with columnar jointing (Excavated thickness is 4.5 m) Layer 9. Brown loam, processed by soil processes (thickness is 1.0 m) Layer 10. Black loam (the modern chernozem soil), penetrated by the roots of herbaceous plants (thickness is 0.3 m).

Radiocarbon date  $31455 \pm 1000$  BP (SPb-2895) (34723–36809 cal BP) corresponded to the layer 3 permitted to identify the interval of Tabulda Horizon. Layers 4–7 and 1–2 possibly also must be included to Tabulda interval (Gornovo IV section).

### 4.2. Insect assemblages from the Gornovo site

Most of the studied fragments (99%) belong to the Coleoptera. Heteroptera and Hymenoptera (Table 3) are poorly represented. Since Heteroptera and Hymenoptera have not been identified to species, they are not used in faunistic analysis. The Coleoptera were assigned to no less than 134 species. Taking into account the materials of the Gornovo II section (Danukalova et al., 2016), the total list of Coleoptera is 142 species of 17 families. The number of species in individual samples differs markedly. The sample S5, where at least 68 species of 16 families were noted, is the richest; the samples S1, S2, and S4 are somewhat poorer (41–51 species each). The sample S7 as well as samples P1 and P2 were the poorest (9–10 species each) (Table 3). It was possible to identify 106 species of 12 families of Coleoptera to a species or species group level (Supplementary Table 2, Figs. 3 and 4). 29 Coleoptera species that were not previously listed for Pleistocene sediments are marked with an asterisk “\*” in Table 3.

A comparison of species composition of Coleoptera from different samples is shown in the similarity graph (Fig. 5). The figure shows that the complexes of species from layers 1–3 (samples S1–S6) of the

Gornovo IV form a rather dense cluster with a similarity level of 35–62%, which is sharply separated (similarity 0–22%) from the complexes of layer 5 Gornovo IV section (sample S7) and layer 2 of the Gornovo II section (samples P1 and P2).

### 4.3. Mollusc assemblages from the Gornovo site

The general list of molluscs consists of 27 species, 20 genera and 14 families (Table 2).

Terrestrial molluscs (8 species) are represented by five families, Succineidae, Pupillidae, Valloniidae, Discidae, Hygromiidae and seven genera.

Freshwater molluscs (16 species) are represented by 12 gastropod species from five families Lymnaeidae, Physidae, Planorbidae, Valvatidae, Bithyniidae, Vivipariidae from 9 genera (Table 2) and by two bivalves' species from the genera *Bithynia* and *Pisidium* of the family Sphaeriidae. The shells of the brackish-water *Pyrgula* cf. *trivialis* Logvinenko et Starobogatov, 1968, *Clessiniola* sp., and *Dreissena polymorpha* (Pallas, 1771) apparently were redeposited from older deposits (Lower Pleistocene).

Mollusc shells are present in the sediments of the Gornovo I–IV sections in different facies. In the sands and interbedded sands and clays that form the lower part of the terrace, molluscs were found in the Gornovo III (layer 4) and the Gornovo II (layer 6). The shells of molluscs are not numerous here, nine shells were found from the Gornovo II and 85 shells of freshwater and terrestrial molluscs from the Gornovo III. The taxonomic composition is mainly formed by freshwater bivalves and gastropods from the eight genera, and terrestrial molluscs belong to *Succinella*, *Pupilla*, and *Vallonia* genera (Table 2). In the lower part of the clay strata of the Gornovo IV (layer 5), three samples with mollusc shells were taken, where 3082 shells of freshwater and terrestrial molluscs have been identified. Taxonomic composition is formed mainly by freshwater and terrestrial molluscs from *Succinella*, *Succinea*, *Oxyloma*, *Pupilla*, and *Vallonia* genera (Table 2). Freshwater bivalves are absent.

The age of samples taken from the upper part of the clay strata (Gornovo II, layers 2, 3; Gornovo I, layer 7; Gornovo I, layer 7) is analogous to the age of samples from the Gornovo II, layer 2 (Fig. 2) (Danukalova et al., 2016). Here, 2557 shells of freshwater and terrestrial molluscs were found and identified. Like the previous one, this is the second largest complex of molluscs.

The taxonomic composition is represented mainly by freshwater gastropods; by single freshwater bivalves *Pisidium* and *Sphaerium*, as well as by numerous terrestrial molluscs (Table 2).

Three samples were taken from the dense loam of the Gornovo I (layers 6, 5) and the Gornovo II (layer 1). These loams occur on blue clays with stumps and numerous eroded organic remains. Molluscs are few in number here, a total of 100 shells were found, and in the samples they are distributed from 6 to 85 specimens (Table 2).

One sample was taken from the upper part of the loess-like loam of the Gornovo I (layer 2). Molluscs are scarce in this sample, a total of 59 shells were found, including redeposited forms (Table 2).

Interpretation of the age of these complexes and their host sediments is presented in the Discussion.

## 5. Discussion

### 5.1. Geochronological/stratigraphical interpretations

The studies of the Gornovo IV section make significant adjustments to the stratigraphic interpretation of the deposits forming the lower part of the high floodplain terrace near Gornovo village.

A radiocarbon date was obtained from layer 3 of the Gornovo IV, which made it possible to correlate the clays of layer 3 with the regional Tabulda Horizon (MIS 3) (the Upper Pleistocene). Earlier, deposits of this level in the Gornovo III and II sections were correlated with the Middle Pleistocene, namely, with the regional Belaya Horizon.



**Table 3**

Subfossil insects from the Gornovo site.

Family	No	Species	N				Nmin									
							Gornovo IV							Gornovo II**		Σ
			H	P	E	O	S1	S2	S4	S5	S6	S7	P1	P2		
Coleoptera																
Carabidae	1	<i>Notiophilus aestuans</i> Dejean, 1826	–	–	2	–	–	1	–	–	–	–	–	–	–	1
	2	<i>Notiophilus aquaticus</i> (Linnaeus, 1758)	–	–	3	–	–	1	1	1	–	–	–	–	3	
	–	<i>Notiophilus</i> sp.	1	2	2	–	–	1	2	2	–	–	–	–	5	
	3	<i>Carabus</i> ? <i>latreillei</i> Fischer von Waldheim, 1820*	–	–	1	–	–	1	–	–	–	–	–	–	1	
	4	<i>Carabus bessarabicus</i> Fischer von Waldheim, 1823*	–	–	1	–	–	–	–	–	1	–	–	–	1	
	–	<i>Carabus</i> sp.	–	2	3	–	2	1	–	1	–	–	–	–	4	
	5	<i>Diacheila polita</i> (Faldermann, 1835)	–	2	–	–	–	–	1	1	–	–	–	–	2	
	6	<i>Elaphrus</i> cf. <i>riparius</i> (Linnaeus, 1758)	–	1	1	–	–	–	1	–	1	–	–	–	2	
	7	<i>Clivina fossor</i> (Linnaeus, 1758)	–	–	4	–	–	–	3	1	–	–	–	–	4	
	8	<i>Dyschiriodes</i> cf. <i>yezoensis</i> Bates, 1883*	–	–	1	–	–	–	1	–	–	–	–	–	1	
	9	<i>Bembidion</i> ( <i>Philochthus</i> ) <i>aeneum</i> Germar, 1823	–	2	5	1	–	–	1	–	–	4	–	–	5	
	10	<i>Bembidion</i> ( <i>Eupetedomus</i> ) sp.	–	–	–	–	–	–	–	–	–	–	–	2	2	
	11	<i>Bembidion</i> ( <i>Plataphus</i> ) <i>difficile</i> (Motschulsky, 1844)	–	–	2	–	1	1	–	–	–	–	–	–	2	
	12	<i>Bembidion</i> ( <i>Plataphus</i> ) <i>gebleri</i> (Gebler, 1833)	–	–	1	–	–	–	–	–	1	–	–	–	1	
	13	<i>Bembidion</i> ( <i>Plataphus</i> ) cf. <i>prasinum</i> (Duftschmid, 1812)	–	–	1	–	–	–	–	1	–	–	–	–	1	
	14	<i>Bembidion</i> ( <i>Blepharoplataphus</i> ) <i>hastii</i> C.R. Sahlberg, 1827	–	–	1	–	–	–	1	–	–	–	–	–	1	
	15	<i>Bembidion</i> ( <i>Peryphus</i> ) <i>dauricum</i> (Motschulsky, 1844)	–	2	9	–	2	2	2	1	2	–	–	–	9	
	16	<i>Bembidion</i> ( <i>Peryphus</i> ) <i>obscurum</i> (Motschulsky, 1845)	–	–	1	–	–	–	–	–	1	–	–	–	1	
	17	<i>Bembidion</i> ( <i>Ocydromus</i> ) cf. <i>grapii</i> Gyllenhal, 1827	–	1	2	–	–	–	–	2	–	–	–	–	2	
	18	<i>Bembidion</i> ( <i>Ocydromus</i> ) <i>yukonum</i> Fall, 1926	–	1	5	–	–	–	2	2	1	–	–	–	5	
	19	<i>Bembidion</i> ( <i>Asioperyphus</i> ) af. <i>infuscatum</i> (Dejean, 1831)	–	–	1	–	–	–	–	1	–	–	–	–	1	
	20	<i>Bembidion</i> ( <i>Pamirium</i> ) ? <i>platypterum</i> Solsky, 1874*	–	–	2	–	–	–	–	–	2	–	–	–	2	
	–	<i>Bembidion</i> spp.	2	11	1	–	1	1	2	7	1	1	–	–	13	
	21	<i>Pogonus punctulatus</i> Dejean, 1828	1	7	16	–	3	5	2	5	–	–	–	–	15	
	22	<i>Patrobus</i> cf. <i>septentrionis</i> Dejean, 1828	–	–	1	–	–	–	–	–	1	–	3	9	13	
	23	<i>Poecilus</i> cf. <i>major</i> (Motschulsky, 1844)	5	29	17	–	8	9	–	7	1	–	–	–	25	
	24	<i>Pterostichus</i> ( <i>Adelosia</i> ) <i>macer</i> (Marshall, 1802)	–	1	1	–	–	–	–	1	–	–	–	–	1	
	25	<i>Pterostichus</i> ( <i>Pseudomaseus</i> ) <i>nigrita</i> (Paykull, 1790)	–	–	–	–	–	–	–	–	–	–	1	–	1	
	26	<i>Pterostichus</i> ( <i>Phonias</i> ) cf. <i>strenuus</i> (Panzer, 1796)	1	4	2	–	–	–	–	–	–	4	1	–	5	
	27	<i>Pterostichus</i> ( <i>Cryobius</i> ) cf. <i>brevicornis</i> (Kirby, 1837)	–	–	2	–	–	1	–	–	–	–	–	–	1	
	28	<i>Pterostichus</i> ( <i>Cryobius</i> ) sp.1	–	–	2	–	–	–	–	–	1	–	–	–	1	
	–	<i>Pterostichus</i> ( <i>Cryobius</i> ) sp.	–	–	2	–	–	–	2	–	–	–	–	–	2	
	29	<i>Pterostichus</i> ( <i>Eosteropus</i> ) <i>mannerheimii</i> (Dejean, 1831)	–	2	–	–	–	1	–	–	–	1	–	–	2	
	30	<i>Pterostichus</i> ( <i>Petrophilus</i> ) <i>kokeilii</i> L. Miller, 1850	–	1	–	–	–	1	–	–	–	–	–	–	1	
	31	<i>Pterostichus</i> ( <i>Petrophilus</i> ) <i>uralensis</i> (Motschulsky, 1850)	–	4	–	–	–	1	1	1	–	–	–	–	3	
	32	<i>Pterostichus</i> ( <i>Petrophilus</i> ) <i>dilutipes</i> (Motschulsky, 1844)	–	–	–	–	–	–	–	–	–	–	1	1	2	
	–	<i>Pterostichus</i> spp.	–	1	3	–	1	–	1	2	–	–	1	–	5	
	33	<i>Amara quenseli</i> (Schönherr, 1806)	–	1	–	–	1	–	–	–	–	–	–	–	1	
	34	<i>Amara</i> sp.1	–	1	–	–	1	–	–	–	–	–	–	–	1	
	35	<i>Cribramara skopini</i> (Hieke, 1976)*	–	1	–	–	–	–	1	–	–	–	–	–	1	
	36	<i>Agonum</i> ( <i>Agonum</i> ) <i>muelleri</i> (Herbst, 1784)	–	–	–	–	–	–	–	–	–	–	6	–	6	
	37	<i>Agonum</i> ( <i>Olisares</i> ) <i>duftschmidii</i> J. Schmidt, 1994	–	–	–	–	–	–	–	–	–	–	6	3	9	
	38	<i>Agonum</i> ( <i>Olisares</i> ) <i>versutum</i> Sturm, 1824	–	–	–	–	–	–	–	–	–	–	13	2	15	
	39	<i>Agonum</i> ( <i>Europhilus</i> ) <i>fuliginosum</i> (Panzer, 1809)	–	–	–	–	–	–	–	–	–	–	1	–	1	
	40	<i>Agonum</i> ( <i>Europhilus</i> ) <i>micans</i> (Nicolai, 1822)	–	–	–	–	–	–	–	–	–	–	3	2	5	
	–	<i>Agonum</i> sp.	–	–	2	1	–	–	–	–	–	1	1	–	2	
	41	<i>Limodromus assimilis</i> (Paykull, 1790)	–	1	–	–	–	–	1	–	–	–	–	–	1	
	42	<i>Platynus livens</i> (Gyllenhal, 1810)	–	2	1	–	–	–	–	–	–	2	1	8	11	
	43	<i>Harpalus</i> ? <i>major</i> (Motschulsky, 1850)*	–	1	–	–	1	–	–	–	–	–	–	–	1	
	44	<i>Harpalus amputatus</i> (Say, 1830)	–	1	–	–	–	–	–	–	1	–	–	–	1	
	45	<i>Harpalus</i> sp. 1	–	1	–	–	–	1	–	–	–	–	–	–	1	
	46	<i>Cymindis kasakh</i> Kryzhanovskij et Emetz, 1973*	2	3	3	–	2	2	–	2	1	–	–	–	7	
	47	<i>Cymindis</i> sp. 1	–	1	–	–	1	–	–	–	–	–	–	–	1	
	–	<i>Cymindis</i> spp.	–	1	–	–	–	–	–	1	–	–	–	–	1	
	–	Carabidae indet.	3	1	4	3	–	–	1	1	–	4	–	–	6	
Helophoridae	48	<i>Helophorus obscurus</i> Poppius, 1907	–	–	1	–	–	–	–	1	–	–	–	–	1	
	–	<i>Helophorus</i> sp.	–	–	4	–	–	–	2	1	–	–	–	–	3	
Hydrophilidae	49	Hydrophilidae indet.	–	3	–	–	–	–	1	1	1	–	–	–	3	
Histeridae	50	<i>Hypocacculus</i> cf. <i>tigris</i> (Marseul, 1862)*	–	–	1	–	–	–	–	1	–	–	–	–	1	
Leiodidae	51	Cholevinae indet.	–	–	1	–	–	–	–	1	–	–	–	–	1	
Silphidae	52	<i>Aclypea altaica</i> (Gebler, 1830)	–	1	2	–	–	–	–	–	3	–	–	–	3	
	53	<i>Aclypea</i> cf. <i>opaca</i> (Linnaeus, 1758)	–	2	1	–	1	1	–	–	–	–	–	–	2	
	–	<i>Aclypea altaica</i> /A. <i>opaca</i>	–	1	–	–	–	–	–	–	1	–	–	–	1	
	54	<i>Aclypea bicarinata</i> (Gebler, 1830)	–	–	10	–	1	–	2	2	3	–	–	–	8	
	55	<i>Aclypea sericea</i> (Zubkov, 1833)	–	16	12	–	3	2	5	5	4	–	–	–	19	
	–	<i>Aclypea</i> spp.	1	–	3	–	1	–	–	1	–	–	–	–	2	
	–	Silphidae indet.	1	1	–	3	–	–	2	1	1	–	–	–	4	
Staphylinidae	56	<i>Eusphalerum</i> sp.	–	1	–	–	–	–	–	1	–	–	–	–	1	
	57	<i>Lathrobium</i> sp.	1	–	–	–	–	–	–	1	–	–	–	–	1	

(continued on next page)

Table 3 (continued)

Family	No	Species	N				Nmin							Gornovo II**		Σ
							Gornovo IV									
			H	P	E	O	S1	S2	S4	S5	S6	S7	P1	P2		
Scarabaeidae	58	<i>Quedius limbatus</i> (Heer, 1839)/ <i>Q. sublimbatus</i> Mäklin, 1853	–	1	–	–	–	–	–	1	–	–	–	–	1	
	59	<i>Quedius mesomelinus</i> (Marsham, 1802)	–	–	1	–	–	–	–	–	1	–	–	–	1	
	–	Staphylinidae indet.	–	–	1	–	–	–	–	1	–	–	–	–	1	
	60	<i>Aphodius (Chilothorax)</i> cf. <i>planus</i> D. Koshantschikov, 1894*	–	–	6	–	2	–	2	1	–	–	–	–	5	
	61	<i>Aphodius (Chilothorax) distinctus distinctus</i> (O.F. Müller, 1776)	–	–	1	–	1	–	–	–	–	–	–	–	1	
	62	<i>Aphodius (Chilothorax) melanostictus</i> W.L.E. Schmidt, 1840	–	–	2	–	1	–	1	–	–	–	–	–	2	
	63	<i>Aphodius (Bodilopsis) sordidus sordidus</i> (Fabricius, 1775)	–	–	3	–	–	–	–	2	1	–	–	–	3	
	64	<i>Aphodius (Phaephodius) rectus</i> (Motschulsky, 1866)	1	–	2	–	1	–	1	1	–	–	–	–	3	
	65	<i>Aphodius (Nialus) varians</i> Duftschmid, 1805*	–	–	3	–	1	–	1	–	–	–	–	–	2	
	66	<i>Aphodius (Planolinellus) cf. vittatus</i> Say, 1825*	–	–	3	–	–	–	1	1	–	–	–	–	2	
Buprestidae	67	<i>Aphodius (Liothorax) plagiatus</i> (Linnaeus, 1767)	1	–	–	–	–	–	1	–	–	–	–	–	1	
	68	<i>Aphodius serotinus</i> (Panzer, 1799)/ <i>A. quadriguttatus</i> (Herbst, 1783)*	–	–	7	–	–	1	1	3	2	–	–	–	7	
	–	<i>Aphodius</i> spp.	7	1	3	–	1	–	2	5	–	–	–	–	8	
	69	<i>Aegialia (Psammoporus) cf. abdita</i> (Nikritin, 1975)	1	2	1	–	–	–	1	1	–	–	–	–	2	
	70	<i>Anthaxia?</i> sp.	–	–	1	–	–	–	1	–	–	–	–	–	1	
	Byrrhidae	71	<i>Porcinolus murinus</i> (Fabricius, 1794)	–	1	2	–	1	1	–	1	–	–	–	3	
	72	<i>Morychus</i> sp.	–	–	1	–	1	–	–	–	–	–	–	–	1	
	Elateridae	73	<i>Berninelsonius hyperboreus</i> (Gyllenhal, 1827)	–	1	1	–	–	–	–	1	–	–	–	–	1
		74	<i>Hypnoidus</i> cf. <i>rivularius</i> (Gyllenhal, 1808)	–	–	–	1	–	–	–	1	–	–	–	–	1
	Anthicidae	75	<i>Limoni</i> cf. <i>obiensis</i> Tsherepanov, 1966*	–	–	2	1	–	–	–	1	–	–	–	–	1
–		Elateridae indet.	–	–	1	–	–	–	1	–	–	–	–	–	1	
76		Anthicidae indet.	–	2	–	–	–	1	–	1	–	–	–	–	2	
Tenebrionidae		77	<i>Centorus rufipes</i> (Gebler, 1833)	–	–	2	–	–	–	–	1	–	–	–	–	1
		78	<i>Centorus</i> cf. <i>procerus</i> (Mulsant, 1854)	–	–	1	–	–	–	–	1	–	–	–	–	1
79		<i>Centorus</i> sp.1	–	–	1	–	–	–	–	1	–	–	–	–	1	
–		<i>Centorus</i> spp.	7	3	6	–	3	1	1	4	2	–	–	–	11	
Chrysomelidae		80	<i>Pedinus</i> cf. <i>femoralis</i> (Linnaeus, 1767)*	1	1	–	–	1	1	–	–	–	–	–	–	2
		81	<i>Anatolica abbreviata</i> (Gebler, 1832)*	2	1	–	–	–	–	–	2	–	–	–	–	2
		82	<i>Donacia bicolora</i> Zschach, 1788	–	–	1	–	1	–	–	–	–	–	–	–	1
	83	<i>Crepidodera</i> sp.	–	–	1	–	1	–	–	–	–	–	–	–	1	
	84	<i>Colaphellus hoeftii</i> (Ménétriés, 1832)	–	1	–	–	1	–	–	–	–	–	–	–	1	
	85	<i>Chrysolina</i> cf. <i>polita</i> (Linnaeus, 1758)*	–	1	–	–	–	1	–	–	–	–	–	–	1	
	86	<i>Chrysolina purpurata</i> (Faldermann, 1833)	–	1	1	–	–	–	–	1	1	–	–	–	2	
	–	<i>Chrysolina</i> sp.	–	1	–	–	1	–	–	–	–	–	–	–	1	
	Brentidae	87	<i>Phaedon?</i> sp.	–	–	2	–	–	–	1	–	–	–	–	–	1
		88	<i>Taphrotopium steveni</i> (Gyllenhal, 1839)	–	–	2	–	1	1	–	–	–	–	–	–	2
Curculionidae	89	<i>Pseudaplemonus martjanovi</i> (Faust, 1891)*	–	–	14	–	3	1	2	3	1	–	–	–	10	
	90	<i>Aizobius sedi</i> (Germar, 1818)*	–	–	2	–	–	1	1	–	–	–	–	–	2	
	91	<i>Pseudoprotapion astragali</i> (Paykull, 1800)	1	–	–	–	1	–	–	–	–	–	–	–	1	
	92	<i>Hemitrichapion</i> sp.	–	–	1	–	–	–	–	1	–	–	–	–	1	
	93	<i>Oxystoma</i> sp.	–	2	–	–	–	–	–	2	–	–	–	–	2	
	94	<i>Eutrichapion</i> (s.str.) sp.	1	1	1	–	–	–	–	2	–	–	–	–	2	
	95	Apioninae indet., sp.1	–	–	1	–	–	1	–	–	–	–	–	–	1	
	96	Apioninae indet., sp.2	–	–	1	–	–	–	–	1	–	–	–	–	1	
	97	Apioninae indet., sp.3	–	–	1	–	–	–	–	1	–	–	–	–	1	
	98	Apioninae indet., sp.4	–	–	1	–	–	1	–	–	–	–	–	–	1	
	99	<i>Tournotaris bimaculata</i> (Fabricius, 1787)	12	6	39	–	6	5	2	8	1	3	–	2	27	
	100	<i>Notaris aethiops</i> (Paykull, 1792)	4	1	1	–	1	4	–	–	–	–	–	–	5	
	101	<i>Thryogenes festucae</i> (Herbst, 1795)	–	–	1	–	–	–	–	–	–	1	–	–	1	
	102	<i>Bagous</i> sp.	1	–	2	–	1	–	1	1	–	–	–	–	3	
	103	<i>Hylobius abietis</i> (Linnaeus, 1758)	–	1	2	–	1	1	–	1	–	–	–	1	4	
	104	<i>Hylobius excavatus</i> (Laicharting, 1781)	–	2	1	–	1	–	1	–	–	–	–	–	2	
	105	<i>Pissodes ?piniphilus</i> (Herbst, 1795)	–	–	1	–	–	–	–	1	–	–	–	–	1	
	106	<i>Pissodes gyllenhalii</i> (C.R. Sahlberg, 1834)	–	–	1	–	–	1	–	–	–	–	–	–	1	
	–	<i>Pissodes</i> sp.	–	–	1	–	–	–	–	1	–	–	–	–	1	
	–	<i>Coniocleonus/Stephanocleonus</i> spp.	1	10	12	1	1	3	2	2	1	–	–	–	9	
	107	Cleonini indet., sp.1	–	–	–	1	1	–	–	–	–	–	–	–	1	
	108	Cleonini indet., sp.2	–	–	–	1	–	1	–	–	–	–	–	–	1	
	109	<i>Aulacobaris lepidii</i> (Germar, 1823)	1	1	4	–	–	2	2	1	–	–	–	–	5	
	110	<i>Baris analis</i> (Olivier, 1791)*	–	–	1	–	–	–	–	1	–	–	–	–	1	
	111	<i>Amalus scorillum</i> (Herbst, 1795)	–	–	3	–	1	–	1	1	–	–	–	–	3	
	112	<i>Ceutorhynchus querceti</i> (Gyllenhal, 1813)*	–	–	1	–	–	–	–	–	1	–	–	–	1	
	113	<i>Anthypurinus basicornis</i> (Schultze, 1898)*	–	–	1	–	–	–	–	1	–	–	–	–	1	
	114	Ceutorhynchini indet., sp.1	–	–	1	–	–	–	–	1	–	–	–	–	1	
	115	<i>Tychius</i> cf. <i>flavus</i> Becker, 1864*	–	1	1	–	1	–	–	1	–	–	–	–	2	
	116	<i>Tychius</i> cf. <i>picrostris</i> (Fabricius, 1787)	–	2	–	–	1	–	1	–	–	–	–	–	2	
	117	<i>Tychius</i> cf. <i>subsulcatus</i> Tournier, 1874*	–	1	6	–	1	–	2	1	1	–	–	–	5	
	–	<i>Tychius</i> sp.	–	–	2	–	–	1	–	1	–	–	–	–	2	
	118	<i>Sibinia stacticis</i> (Becker, 1864)*	–	–	1	–	1	–	–	–	–	–	–	–	1	

(continued on next page)

Table 3 (continued)

Family	No	Species	N				Nmin								Gornovo II**		Σ
							Gornovo IV										
			H	P	E	O	S1	S2	S4	S5	S6	S7	P1	P2			
Scolytidae	119	<i>Sibinia subelliptica</i> Desbrochers des Loges, 1873*	–	–	3	–	–	–	1	2	–	–	–	–	3		
	120	<i>Sibinia unicolor</i> (Fahraeus, 1843)*	–	–	1	–	–	1	–	–	–	–	–	–	1		
	121	<i>Hypera</i> sp.	–	1	–	–	–	–	1	–	–	–	–	–	1		
	122	<i>Pachypera</i> sp.	3	–	–	–	–	–	1	–	2	–	–	–	3		
	123	<i>Metadonus</i> sp.1	–	1	–	–	–	–	1	–	–	–	–	–	1		
	124	<i>Phyllobius pomaceus</i> Gyllenhal, 1834	–	4	–	–	2	1	–	–	–	–	–	–	3		
	125	<i>Phyllobius</i> sp.1	–	–	–	1	–	–	–	1	–	–	–	–	1		
	–	<i>Phyllobius</i> sp.	–	–	4	–	1	–	2	–	–	–	–	–	3		
	126	<i>Polydrusus amoenus</i> (Germar, 1823)	1	–	–	–	1	–	–	–	–	–	–	–	1		
	127	<i>Polydrusus cervinus</i> (Linnaeus, 1758)*	–	–	2	–	–	–	–	2	–	–	–	–	2		
	128	<i>Ptochus porcellus</i> Boheman, 1834*	–	–	1	–	1	–	–	–	–	–	–	–	1		
	129	<i>Otiorhynchus bardus</i> Boheman, 1842	–	–	62	–	3	1	13	14	6	–	–	–	37		
	130	<i>Otiorhynchus</i> af. <i>ursus</i> Gebler, 1844	–	–	94	–	12	16	12	8	5	–	–	–	53		
	–	<i>Otiorhynchus bardus</i> /O. af. <i>ursus</i>	57	81	3	–	31	18	8	21	2	–	–	–	80		
	131	<i>Otiorhynchus arcticus</i> (Fabricius, 1780)	–	2	–	–	–	–	1	1	–	–	–	–	2		
	132	<i>Otiorhynchus</i> cf. <i>janovskii</i> Korotyaev, 1990	–	–	1	–	–	–	1	–	–	–	–	–	1		
	133	<i>Otiorhynchus concinnus</i> Gyllenhal, 1834*	1	1	–	–	1	1	–	–	–	–	–	–	2		
	134	<i>Otiorhynchus nodosus</i> (Müller, 1764)	2	1	–	–	1	–	–	1	–	–	–	–	2		
	135	<i>Otiorhynchus politus</i> Gyllenhal, 1834	3	3	2	–	1	2	–	–	1	–	–	–	4		
	136	<i>Parameira</i> sp.	–	–	2	–	–	–	–	1	–	–	–	–	1		
	137	<i>Simo</i> sp.	–	–	1	–	1	–	–	–	–	–	–	–	1		
	138	Curculionidae indet., sp.1	1	–	–	–	–	1	–	–	–	–	–	–	1		
	139	Curculionidae indet., sp.2	–	1	–	–	–	–	1	–	–	–	–	–	1		
	140	Curculionidae indet., sp.3	–	–	1	–	–	–	–	1	–	–	–	–	1		
	–	Curculionidae indet.	1	–	28	2	2	1	3	11	3	–	–	–	20		
	141	<i>Phloeotribus spinulosus</i> (Rey, 1883)	–	–	7	–	1	1	1	2	1	–	–	–	6		
142	<i>Hylastes</i> sp.	–	–	1	–	–	–	–	–	1	–	–	–	1			
–	–	Coleoptera indet.	1	1	12	1	1	–	1	4	5	1	–	12			
Coleoptera in all			129	255	532	18	107	82	96	129	59	19	36	30	558		
Number of Coleoptera species			33	72	116	13	51	41	49	68	33	9	10	9	142		
Heteroptera																	
Pentatomidae	143	Pentatomidae indet.	–	1	–	–	1	–	–	–	–	–	–	–	1		
–	–	Heteroptera indet.	1	–	–	–	–	–	–	1	–	–	–	–	1		
Hymenoptera																	
Tenthredinidae	144	Tenthredininae indet.	–	–	–	1	1	–	–	–	–	–	–	–	1		
–	145	Hymenoptera indet.	1	–	–	1	–	1	–	1	–	–	–	–	2		
–	–	Insecta indet.	–	–	–	4	1	–	1	–	1	–	–	–	3		

N – number of fragments: H – head, P – pronotum, E – elytron, O – other fragments. S1–S7 samples from the section IV. \*species records for Pleistocene deposit for the first time. \*\* – samples P1 and P2 from the Gornovo II section (Danukalova et al., 2016).

Between layers 1–4 and layer 5 of the Gornovo IV section, a sequential change of sedimentation environments is observed from river/floodplain (interbedded clay and sand) to oxbows (clay). Therefore, sediments from layers 1–4 and layer 5 have not evident stratigraphic break.

The entomofauna from layers 1–3 includes both thermo- and cryophilic species, which indicates a high continental climate. At the same time, according to the most cold-loving species, characteristic of the tundra, the average July air temperatures were reconstructed not higher than +15 °C. In layer 5 (as well as in layer 2 of the Gornovo II section), softer and warmer conditions are reconstructed by insects. Taking into account the age of layer 3, it is more likely to assume that the sediments of layers 1–4 accumulated in the middle of the Tabulda time, and insects were buried during the cold substages of MIS 3 (Laukhin et al., 2015). Among plant macroremains, Dorofeev previously noted the presence of some glacial forms (Yakhemovich et al., 1987; Danukalova et al., 2016), which is consistent with the data on insects. Regarding the interpretation of age, Dorofeev believed that the plants were Middle Pleistocene and the flora was glacial (MIS 10).

Remains of large mammals of the Khazar faunistic complex found in the Gornovo site were studied by Yakhemovich et al. (1987) and Danukalova et al. (2016), which attributed them to the Belaya (or Likhvin) deposits (end of the Middle Pleistocene) in the so-called Singil complex, which influenced the assignment of the sands of the lower part of the section. However, as convincingly shown for the Volga sites (Zastrozhenov et al., 2018, 2020, 2021), the Singil complex is much younger

than previously understood. It corresponds to the end of the Middle Pleistocene, and, most likely, it persisted into the beginning of the Late Pleistocene. In the Fore-Urals, at the beginning of the Late Pleistocene, the terrain uplifted and rivers were deepening (Puchkov and Danukalova, 2009; Yakovlev et al., 2013). Incision (bottom erosion) and followed lateral erosion, which led to the destruction of river terraces and redeposition of the fossils they contained. It is quite possible that the large mammal remains found on the river bank are not of Likhvin (the Middle Pleistocene), but of the beginning of the Late Pleistocene.

The stratigraphic subdivision of the first above-floodplain terrace into two regional horizons, the Tabulda and Kudashevo (Upper Pleistocene), fully corresponds to the previous reconstructions suggesting the correlation of river terraces with the stratigraphic horizons of the Pleistocene, those based on radiocarbon dates and the faunas of small mammals published earlier (Danukalova et al., 2006; Danukalova, 2010; Yakovlev et al., 2013).

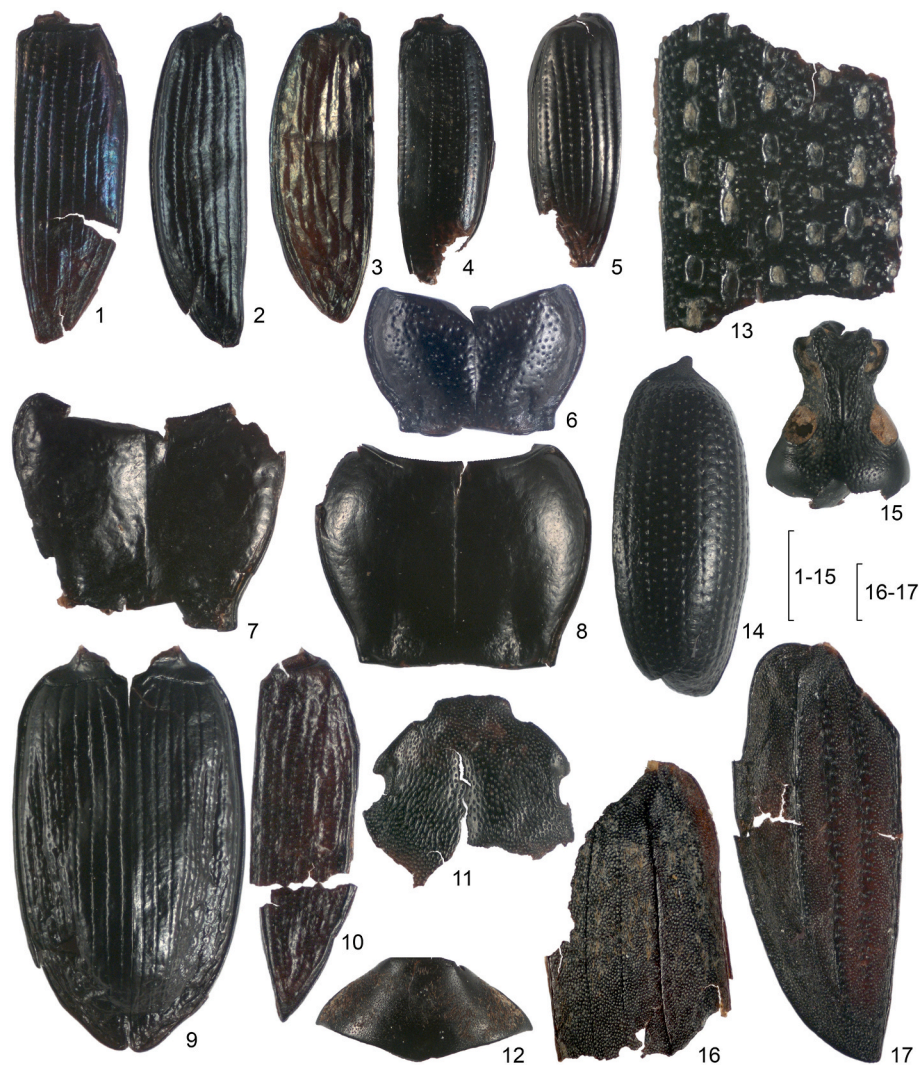
Taking into account the previous publications and new data, the interpretation of the Gornovo site is shown in Fig. 2.

## 5.2. Taxonomic composition of insect assemblages

### 5.2.1. Family Carabidae

In the general list of Coleoptera of the Gornovo site, the family of ground beetles (Carabidae) prevails – 47 species, 33%. They account for approximately the same proportion (from 22 to 36%) in samples S1–S6, but in the samples S7, P1, and P2, the prevalence of ground beetles is





**Fig. 3.** Carabidae (1–9), Tenebrionidae (10–11), Byrrhidae (12), Curculionidae (13–15), and Silphidae (16–17) fragments from the Gornovo IV section. 1 – *Pogonus punctulatus* (S5), 2 – *Bembidion hastii* (S4), 3 – *B. gebleri* (S6), 4 – *Notiophilus aestuans* (S2), 5 – *Dyschiriodes cf. yezoensis* (S4), 6 – *Cribramara skopini* (S4), 7 – *Pterostichus macer* (S5), 8 – *Poecilus cf. major* (S2), 9 – *Pterostichus (Cryobius) sp.* (S6), 10 – *Centorus rufipes* (S5), 11 – *Anatolica abbreviata* (S5), 12 – *Porcinolus murinus* (S1), 13 – *Hylobius excavatus* (S4), 14 – *Otiorynchus af. ursus* (S1), 15 – *O. concinnus* (S1), 16 – *Aclypea altaica* (S6), *A. sericea* (S5). 1–5, 9–10, 13–14, 16–17 – elytra, 6–8, 12 – pronotum, 11, 15 – head. Scale bars 1 mm.

even more pronounced – from 56 to 100% (Fig. 6A). In the samples S1–S6, three species can be distinguished, which are the most numerous and represented almost in all samples (*Bembidion dauricum* (Motschulsky, 1844), *Pogonus punctulatus* Dejean, 1828, *Poecilus cf. major* (Motschulsky, 1844)). These species are characteristic for the Pleistocene deposits of the south of West Siberia (Zinovyev et al., 2016; Gurina et al., 2019a, b). Ground beetles from the sample S7 and, especially from the samples P1 and P2, noticeably differ from the previous assemblages. *Platynus livens* (Gyllenhal, 1810) was recorded in all three samples. This species has not been previously recorded in the Quaternary deposits of West Siberia and Eastern Europe. The last two samples also contain numerous species of the tribe Platynini from the genus *Agonum*, which are absent in other samples.

Seven species of ground beetles have not been previously recorded in the Pleistocene sediments. Among them *Cymindis kasakh* Kryzhanovskij et Emetz (1973) (Figs. 4, 1) and *Cribramara skopini* (Hieke, 1976) (Figs. 3, 6) recorded from singletons in the samples S1–S6. Both are little known species in the recent fauna that are available only from a few specimens from Northwestern Kazakhstan and the extreme Southeast of European Russia (Emetz, 1973; Hieke, 1976; Makarov et al., 2009; Kabak and Dudko, 2021). Other species are the European steppe species *Carabus bessarabicus* Fischer von Waldheim, 1823, and three eastern species *Carabus latreillei* Fischer von Waldheim, 1820, *Harpalus major* (Motschulsky, 1850), *Dyschiriodes cf. yezoensis* Bates, 1883. *C. bessarabicus* and *H. major* are questionable, since their identification

from the presented base of the elytron and incomplete pronotum is unreliable. The Far Eastern species *Dyschiriodes yezoensis* is a vicariate of the Central Palaearctic *D. longicollis* (Motschulsky, 1844) and the West Palaearctic *D. neresheimeri* (Wagner, 1915), from which it differs mainly in the absence of microsculpture on the basal inclination of elytra (Fedorenko, 1996). It is possible that in the Late Pleistocene (MIS 3) these species have not yet diverged from each other, but the well-preserved elytron from the sample S4 (Figs. 3, 5) corresponds precisely to the Far Eastern form. One more species, *Bembidion cf. platypterum* Solsky, 1874, undoubtedly belongs to the subgenus *Pamirium*, which is widespread in the mountains of Middle and Central Asia and is represented by many closely related species that reliably differ from each other only in the structure of male genitalia (Mikhailov, 1988).

### 5.2.2. Family Curculionidae

With at least 42 species, the family of weevils (Curculionidae) is represented in the Gornovo site only slightly poorer than ground beetles. In the samples S1–S5 it prevails in the number of species (31–39%), in the samples S6 and S7 they also constitute a significant proportion (27–33%) after ground beetles. They are represented by singletons in the sample P2 and absent in the sample P1 (Fig. 6A). In terms of the number of individuals (*Nmin*), two closely related species, *Otiorynchus af. ursus* Gebler, 1844 (Fig. 3, 14) and *O. bardus* Boheman, 1842 predominate in the samples S1–S6). In total, in these samples they account for 42–58% of Curculionidae and 16–29% of all Coleoptera. These species are



**Fig. 4.** Carabidae (1–3), Scolytidae (4), Histeridae (5), Curculionidae (6–12), and Brentidae (13–15) fragments from the Gornovo site. 1 – *Cymindis kasakh* (S1), 2 – *Diacheila polita* (S4), 3 – *Bembidion aeneum* (S7), 4 – *Phloeotribus spinulosus* (S5), 5 – *Hypocaccus cf. tigris* (S5), 6 – *Sibinia staticis* (S1), 7–9 – *Aulacobaris lepidii* (S2, S4), 10 – *Anthypurinus basicornis* (S5), 11 – *Thryogenes festucae* (S7), 12 – *Amalus scortillum* (S4), 13 – *Aizobius sedi* (S2), 14 – *Pseudaplemonus martjanovi* (S4), 15 – *Taphrotopium steveni* (S1). 1–3, 8 – pronotum, 4–7, 10–15 – elytra, 9 – head. Scale bar 1 mm.

reliably distinguished only in punctuation of the elytra. They are indistinguishable in the structure of the head and pronotum, which complicates interpretation. At the same time, *Otiorhynchus* af. *ursus* is predominantly represented in the samples S1 and S2 where *O. bardus* was recorded singly, while in the samples S4–S6 these species were found in approximately equal proportions (Table 3). These species are prevalent in Late Pleistocene deposits of the south of West Siberian Plain and have local ranges in the recent fauna (Legalov et al., 2016). Generally these groups remain poorly studied. On some fragments of the sub-fossil elytra of *O. af. ursus*, pubescence is well preserved and is noticeably shorter than in typical recent *O. ursus* (= *O. kasachstanicus* Arnoldi, 1964) from Central Kazakhstan. Similar specimens with short pubescence are known from the highlands of Western Altai and Tarbagatai range in East Kazakhstan. The additional material is required to decide on the status of those populations. Until recently the questions associated with the name *O. bardus* Boheman, 1842 have existed. The study of type specimens of this and other closely related species made it possible to establish synonymy: *O. bardus* Boheman, 1842 = *O. altaicus* Stierlin, 1861 = *O. karkaralensis* Bajtenov, 1974 (Legalov, 2020).

The weevil species composition of the Gornovo site is highly specific. Of them, 11 species were not previously known from the Pleistocene (Table 3). Except boreal *Ceutorhynchus querceti* (Gyllenhal, 1813), nearly all of these species are now widespread in the steppe zone of Eurasia, much to the south of the Gornovo site.

#### 5.2.3. Family Brentidae

Brentidae is the third most represented family in the site. At least 11 species from the subfamily Apioninae were recovered (samples S1–S6; Fig. 6A). Four species were identified, including *Pseudaplemonus martjanovi* (Faust, 1891) (Figs. 4, 14; 8) and *Aizobius sedi* (Germar, 1818)

(Figs. 4, 13), previously unknown from Pleistocene deposits (Table 3).

#### 5.2.4. Family Scarabaeidae

The family Scarabaeidae in the site is represented by no less than nine species of the genus *Aphodius* and one species *Aegialia* cf. *abdita* (Nikritin, 1975) (Fig. 6A). The species of the genus *Aphodius* are numerous (samples S1, S4, S5), present as singletons (S2 and S6), and not found in the other samples (S7, P1, P2). Four *Aphodius* species are reported for the first time for the Pleistocene (Table 3), but two of them are also found in the sediments of the south of the West Siberian Plain (unpublished data). *Aphodius varians* Duftschmid, 1805 и *A. cf. vittatus* Say, 1825 are so far known only from Gornovo site.

#### 5.2.5. Family Silphidae

Family Silphidae is represented by a significant number of fragments ( $N_{min} = 19$ ), including four species of the genus *Aclypea*. Of them, *A. sericea* (Zubkov, 1833), a characteristic species in the Late Pleistocene faunas of the south of Western Siberia (Tsepelev et al., 2013), was the most numerous.

The remaining 13 beetle families found in the Gornovo site are represented by a small number of species (samples S1–S6; Table 3).

Thus, according to the taxonomic composition of Coleoptera, the entomocomplexes of layer 5 Gornovo IV (sample S7) and layer 2 Gornovo II (samples P1 and P2) are sharply distinguished and characterized by a significant predominance of ground beetles and their unique species composition. Insect assemblages from layers 1–3 (samples S1–S6) of the Gornovo IV are similar to each other and are characterized by high taxonomic diversity with a predominance of Curculionidae and Carabidae, especially *Otiorhynchus* af. *ursus* and *O. bardus*.



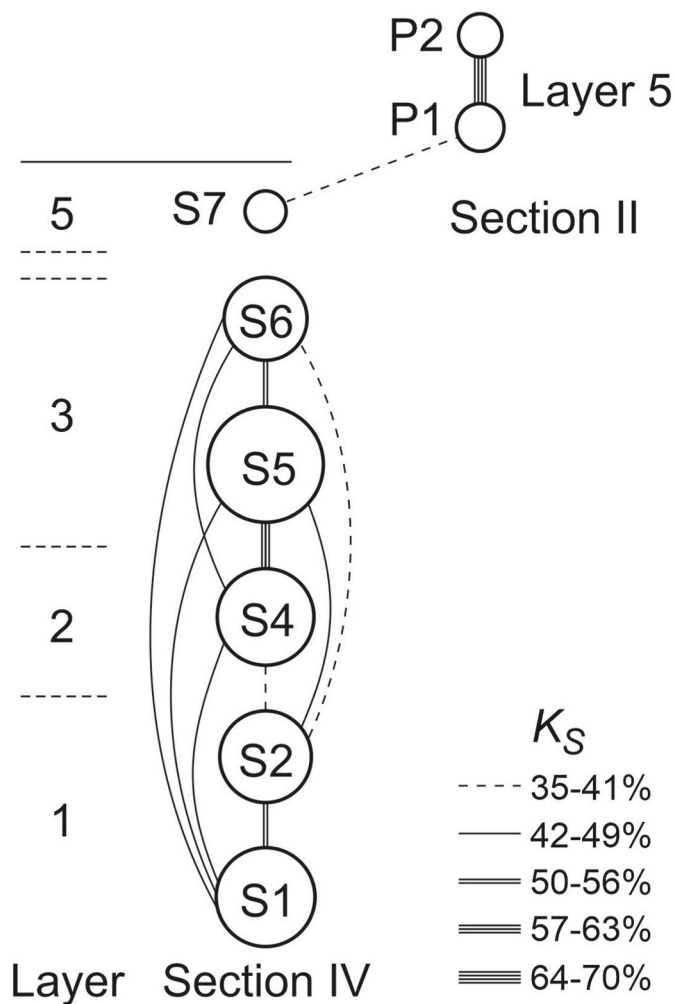


Fig. 5. Similarity graph of insect assemblages from the samples of Gornovo II and Gornovo IV.

### 5.3. Trophic groups of insects

Predatory beetles are present in all samples from the Gornovo site (Fig. 6B). They are relatively few (14% of species) in the sample S1, 26–39% in the samples S2–S6, while in the samples S7, P1 and P2 they, on the contrary, form the basis of taphocoenosis (63–100%). The overwhelming majority of the noted species are non-specialized predators (Carabidae, Staphylinidae and Histeridae). The intermediate group between predators and herbivorous beetles is made up of mixophagous ground beetles (*Amara*, *Cribramara* and *Harpalus*). At the adult stage, they are mainly herbivorous, eating seeds and young shoots, but their larvae are predacious (Kryzhanovskij, 1983).

Phytophagous Coleoptera predominate in the samples S1–S6 and are represented here by the families Curculionidae, Brentidae, Chrysomelidae, Silphidae, Tenebrionidae, Byrrhidae, and Scolytidae. There are especially many herbivorous species in the sample S1, where they make up 69% (Fig. 6B). The species of Tenebrionidae and Silphidae found in the sediments, as well as some Curculionidae and Chrysomelidae, are polyphagous that feed on plants of various families. Oligo- and, especially, monophagous are more interesting, since they are more significant for the reconstructions of the natural environment. Due to the close relationship of some herbivores with certain plants, in addition to the insects, our landscape reconstructions also include host-plants (Table 4). Thus, samples S1–S6 suggest a high diversity of herbaceous vegetation. The sediments contain at least 26 Coleoptera species developing on herbaceous or semi-shrub dicotyledons from nine

families. In all these samples, representatives associated with Plumbaginaceae and Brassicaceae were found. In most samples, the presence of Fabaceae, Caryophyllaceae, Polygonaceae, and Asteraceae is also reconstructed. Based on the list of specialized phytophages from samples S1–S6, we conclude that in all reconstructions, along with meso- and hygrophytic plants (such as *Polygonum*, *Rumex*, *Rorippa palustris*), the following xerophytes were also present and even predominated: *Limonium*, *Goniolimon*, *Sedum*, *Astragalus*, *Dianthus*, *Salsola*, and *Artemisia*. Insect species developing on near-water monocots were found in all samples with phytophagous, including samples S7 and P2. Also, in all samples, four species of Curculionidae and two species of Scolytidae developing on conifers were occasionally noted, of which two species prefer *Pinus sylvestris*, two species prefer *Picea* spp. and one species prefers *Larix* spp. (Table 4). In addition, representatives of the family Byrrhidae, which are closely associated with mosses of the Marchantiophyta, can be classified as specialized phytophagous (Tshernyshev, 2012).

Compared to carnivorous and phytophagous insects, saprophagous constitute a relatively small group, but their ecological significance is important. Saprophagous are found in the samples S1–S6, where their number is 5–22% (Fig. 6B). According to food preferences, a subgroup of detritivores feeding on plant or animal remains can be distinguished (Helophoridae, Hydrophilidae, Leiodidae, Anthicidae, as well as *Aegialia* cf. *abdit* (Scarabaeidae)). The subgroup of coprophages developing mainly in ungulate droppings is even more interesting. This subgroup includes at least nine species of the genus *Aphodius* found in samples S1–S6, with the greatest diversity (seven species) noted in the sample S4 (Table 3). The high diversity and abundance of coprophagous in the sediments indirectly indicates favourable conditions for large mammals, in particular ungulates. At the same time the absence in the sediments of larger representatives of coprophages, which are currently characteristic of arid regions of Kazakhstan and Central Asia (Nikolajev, 1987), is puzzling in view of a question about the decomposition of excrement of the Pleistocene megafauna. No saprophagous were found in the samples S7, P1 and P2, which is probably due to the limited sample size.

### 5.4. Habitats of subfossil beetles

Coleoptera samples of the Gornovo site are characterized by high ecological diversity. Based on the beetle fauna from the samples S1–S6, six types of habitats can be distinguished: steppe, forest, tundra, meadow, near-water and saline. Beetles from the samples S7, P1 and P2 are ecologically more homogeneous and include only near-water, forest, and halophilic representatives.

#### 5.4.1. Steppe habitats

In the samples S1–S6, the species characteristic for steppe biotopes constitute from a quarter to a third of the species composition (Fig. 6C). They belong to eight families of Coleoptera, where most of the species belong to the families Brentidae and Curculionidae (Supplementary Table 2). The high taxonomic diversity of steppe species, in comparison with other ecological groups, suggests a wide distribution of steppe landscapes in the periods corresponding to the formation of sediments. It should also be noted that some species are highly xerophilic, for example, *Taphrotopium steveni* (Gyllenhal, 1839). They likely indicate a semi-desert rather than a steppe complex. No steppe species were found in samples S7, P1 and P2. However, two fragments from sample S7 assigned to the genus *Pachypera*, were not identified to the species level. Some species of *Pachypera* inhabit steppe and tall-grass meadows.

#### 5.4.2. Forest habitats

As shown earlier, in all samples (except P1), xylophilic species developing in coniferous wood were found (Table 4). Specialization of the noted species suggests the coexistence of *Picea*, *Larix*, and *Pinus*. Samples P1 and P2 also contained the remains of *Picea* and *Abies* (Danukalova et al., 2016). However, in addition to a few xylophages,



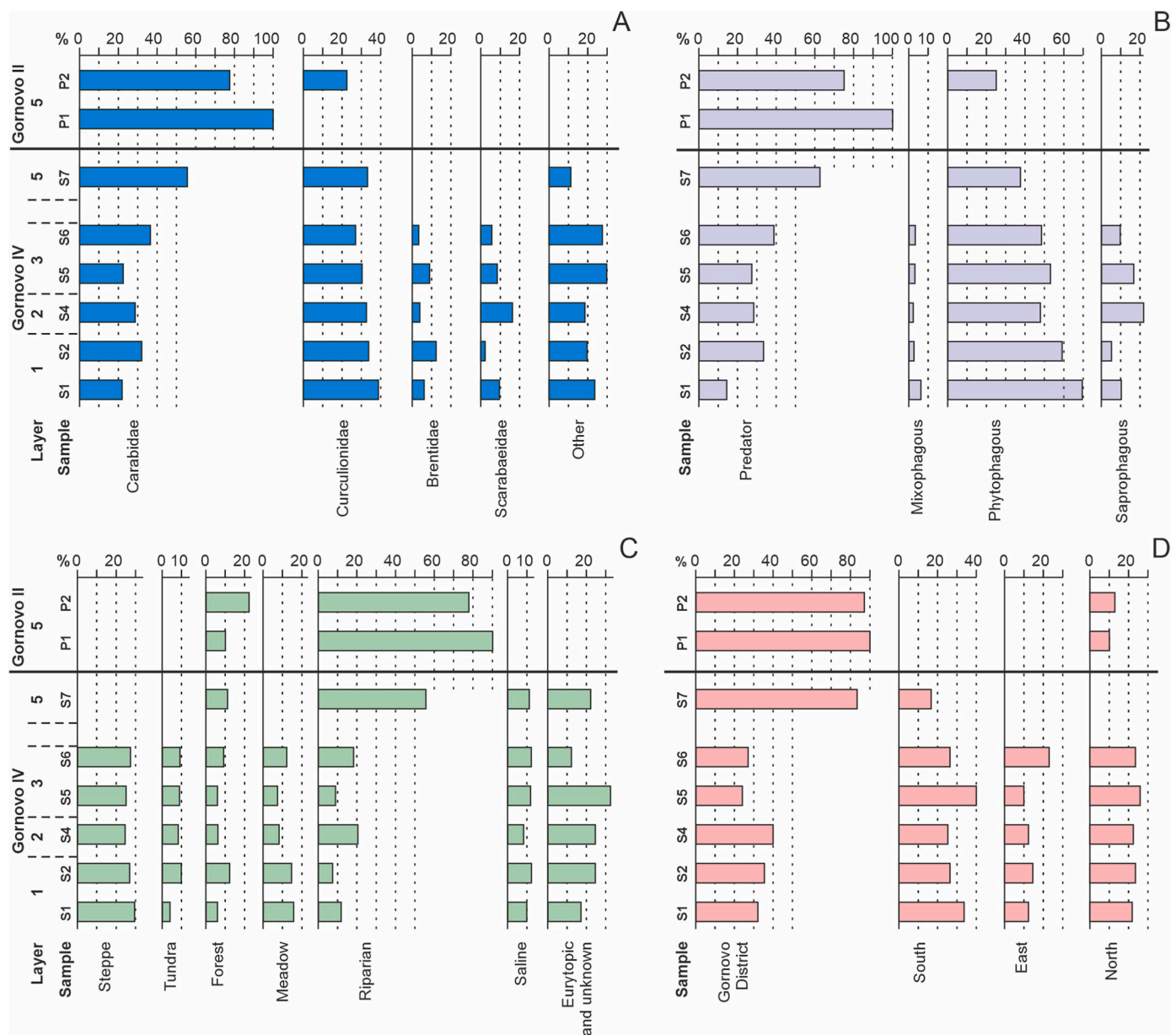


Fig. 6. Species composition of Coleoptera from the Gornovo site. A – taxonomical, B – trophic, C – habitat, D – distribution.

samples S1–S6 revealed only single fragments of species of the forest complex. Typical forest species are carabids *Pterostichus mannerheimii* (Dejean, 1831) and *P. uralensis* (Motschulsky, 1850). They are now abundant in the southern taiga of the Fore-Urals (Vorontin and Gridina, 1984) and were found in the samples S2, S4, S5 (Table 3). *Polydrusus cervinus* (Linnaeus, 1758) (Curculionidae) from the sample S6 is another species belonging to the forest complex (Koch, 1992). Although this species develops on various deciduous trees and shrubs, it is more common on birch. In the samples S7, P1 and P2, forest species are also few. They are the only representatives of zonal habitats. In addition to the samples from the underlying layers the forest complex also includes *P. dilutipes* (Motschulsky, 1844), which is characteristic of the taiga forests of Siberia (Zinovyev, 2007; Khobrakova et al., 2014). In addition, the hygrophilous *Platynus livens* and *Pterostichus strenuus* (Panzer, 1796) are also characteristic inhabitants of wet and swampy areas of deciduous and mixed forests (Lindroth, 1992a). Thus, based on the small proportion of forest species compared with more abundant steppe species, coniferous forests are reconstructed for the landscapes corresponding to the samples S1–S6. They occupied very limited areas, probably in the

river valleys. On the contrary, Coleoptera assemblages from samples S7, P1 and P2 suggest that forests in the region were more widespread than previously assumed (Danukalova et al., 2016).

#### 5.4.3. Tundra or tundra-like habitats

These habitats are reconstructed based on the presence of eight cryophilic species, from the families Carabidae and Elateridae (Supplementary Table 2). Their share is 8–10% in samples S2–S6, about 4% in sample S1, while in samples S7, P1 and P2 they are absent. The species of this group usually inhabit dry (*Bembidion dauricum*, *B. grapii* Gyllenhal, 1827, *Berninelsonius hyperboreus* (Gyllenhal, 1827)) or mesic (*Diacheila polita* (Faldernmann, 1835), *Pterostichus brevicornis*, *P. kokeilii* L. Miller, 1850)) tundra (Lindroth, 1992a; Khobrakova et al., 2014). Through intrazonal biotopes (river valleys, lake shores, wetlands), some of these species penetrate far into the taiga zone (*Pterostichus brevicornis* (Kirby, 1837), *Hypnoidus cf. rivularius* (Gyllenhal, 1808)), and in the mountains of Southern Siberia, *Bembidion dauricum* also occupies meadows of the steppe altitude belt (Khobrakova et al., 2014).

**Table 4**

Host-plant of mono- and oligophagous Coleoptera from the Gornovo deposits.

Host-plant		Coleoptera species	Samples								References
Family	Genera, species		S1	S2	S4	S5	S6	S7	P2		
Pinaceae	Predominantly <i>Pinus sylvestris</i> L.	<i>Hylobius abietis</i> (Linnaeus, 1758)	+	+	–	+	–	–	+	Arnoldi et al. (1974)	
		<i>Pissodes ?piniphilus</i> (Herbst, 1795)	–	–	–	+	–	–	–	Koch (1992)	
	Predominantly <i>Larix</i> Mill.	<i>Hylobius excavatus</i> (Laicharting, 1781)	+	–	+	–	–	–	–	Burakowski et al. (1995)	
		Predominantly <i>Picea</i> A. Dietr.	<i>Pissodes gyllenhalii</i> (C.R. Sahlberg, 1834)	–	+	–	–	–	–	–	Smreczyński (1972)
	<i>Phloeotribus spinulosus</i> (Rey, 1883)		+	+	+	+	+	–	–	Stark (1952)	
		<i>Hylastes</i> sp.	–	–	–	–	+	–	–	Stark (1952)	
Cyperaceae, Poaceae, Typhaceae and other Monocots	–	<i>Tournotaris bimaculata</i> (Fabricius, 1787)	+	+	+	+	+	+	+	Dieckmann (1986); Burakowski et al. (1995)	
	–	<i>Notaris aethiops</i> (Paykull, 1792)	+	+	–	–	–	–	–	Dieckmann (1986)	
	–	<i>Thryogenes festucae</i> (Herbst, 1795)	–	–	–	–	–	+	–	Egorov et al. (1996)	
	–	<i>Donacia bicolora</i> Zschach, 1788	+	–	–	–	–	–	–	Medvedev and Roginskaya, 1988	
Crassulaceae	<i>Sedum</i> L., <i>Sempervivum</i> L.	<i>Aizobius sedi</i> (Germar, 1818)	–	+	+	–	–	–	–	Ehret (1990)	
Fabaceae	<i>Astragalus</i> L.	<i>Pseudoprotapion astragali</i> (Paykull, 1800)	+	–	–	–	–	–	–	Solodovnikova (1963)	
		<i>Tychius</i> cf. <i>subsulcatus</i> Tournier, 1874	+	–	+	+	+	–	–	Caldara (1990); Isajev (2007)	
	<i>Medicago</i> L.	<i>Tychius</i> cf. <i>flavus</i> Becker, 1864	+	–	–	+	–	–	–	Dieckmann (1988)	
	<i>Trifolium</i> L.	<i>Tychius</i> cf. <i>picrostris</i> (Fabricius, 1787)	+	–	+	–	–	–	–	Dieckmann (1988); Egorov et al. (1996)	
	–	<i>Hemirichapion</i> sp., <i>Oxystoma</i> sp., <i>Eutrichapion</i> sp.	–	–	–	+	–	–	–	Alonso-Zarazaga (1990)	
	Salicaceae	<i>Salix</i> L., <i>Populus</i> L.	<i>Crepidodera</i> sp.	+	–	–	–	–	–	–	Medvedev and Roginskaya, 1988
Brassicaceae	<i>Rorippa palustris</i> (L.) Besser	<i>Ceutorhynchus querceti</i> (Gyllenhal, 1813)	–	–	–	–	+	–	–	Smreczyński (1974)	
	–	<i>Colaphellus hoeftii</i> (Ménétriés, 1832)	+	–	–	–	–	–	–	Medvedev and Roginskaya, 1988	
	–	<i>Phaedon</i> sp.	–	–	+	–	–	–	–	Medvedev and Roginskaya, 1988	
	–	<i>Aulacobaris lepidii</i> (Germar, 1823)	–	+	+	+	–	–	–	Zaslavskij (1956)	
Amaranthaceae	<i>Salsola</i> L.	<i>Anthypurinus basicornis</i> (Schultze, 1898)	–	–	–	+	–	–	–	Korotyaev (2005); Korotyaev and Khrisanova, 2009	
Caryophyllaceae	<i>Dianthus</i> L.	<i>Sibinia subelliptica</i> Desbrochers des Loges, 1873	–	–	+	+	–	–	–	Dieckmann (1988)	
	<i>Gypsophila</i> L.	<i>Sibinia unicolor</i> (Fahraeus, 1843)	–	+	–	–	–	–	–	Smreczyński (1972); Isajev (2007)	
Plumbaginaceae	<i>Limonium</i> Mill.	<i>Sibinia staticis</i> (Becker, 1864)	+	–	–	–	–	–	–	Yunakov et al. (2018)	
	<i>Goniolimon</i> Boiss.	<i>Pseudaplemonus martjanovi</i> (Faust, 1891)	+	+	+	+	+	–	–	Korotyaev (1984)	
Polygonaceae	<i>Polygonum</i> L., <i>Rumex</i> L.	<i>Amalus scortillum</i> (Herbst, 1795)	+	–	+	+	–	–	–	Dieckmann (1972)	
Lamiaceae	–	<i>Chrysolina</i> cf. <i>polita</i> (Linnaeus, 1758)	–	+	–	–	–	–	–	Medvedev and Roginskaya, 1988	
Asteraceae	<i>Artemisia</i> L.	<i>Chrysolina purpurata</i> (Faldermann, 1833)	–	–	–	+	+	–	–	Lopatin (2010)	
		<i>Taphrotopium steveni</i> (Gyllenhal, 1839)	+	+	–	–	–	–	–	Kazakova (1972)	
	<i>Pulicaria</i> Gaertn.	<i>Baris analis</i> (Olivier, 1791)	–	–	–	+	–	–	–	Smreczyński (1974); Isajev (2007)	

#### 5.4.4. Mesophytic meadows

Mesophytic meadows are the most typical habitats for mesophilic species characteristic of open landscapes (Supplementary Table 2). Such species make up 5–15% in the samples S1–S6 (Fig. 6C). In the samples S7, P1 and P2, meadow mesophilous were not found. It should be noted that, although mesophytic meadows are more typical for relatively humid regions, for example, the northern forest-steppe of the West Siberian Plain (Mordkovich, 2012), the abundance of meadow species in sediments may also be due to the taphonomic bias. Meadow communities could form only with a moisture gradient from floodplain to dry uplands and were not widespread in the region, despite their relatively good representation in the sample.

#### 5.4.5. Near-water habitats

In the general list of insects of the Gornovo site, the hygrophilous

group is the most numerous and is represented by 30 species (Supplementary Table 2). However, in the samples S1, S4 and S6, the proportion of species of this group does not exceed 20%, and in samples S2 and S5 it is even less than 10%, which is probably due to the taphonomic conditions during deposition. Habitat differentiation within the group is not sharp. The following species are distinguished as characteristic of wet meadows: *Tournotaris bimaculata* (Fabricius, 1787), *Otiorynchus concinnus* Gyllenhal, 1834 (Curculionidae) and *Phaedon* sp. (Chrysomelidae). Three species from the genus *Bembidion* are obligatory associates with gravel shores (*B. gebleri* (Gebler, 1833), *B. cf. prasinum* (Duftschmid, 1812) and *B. hastii* C.R. Sahlberg, 1827) (Lindroth, 1992a; Khobrakova et al., 2014). The majority of species are confined directly to the samples S7, P1 and P2, hygrophilic species predominate sharply (56–90%) and most of them are typical of floodplain hygrophytic meadows of the forest zone.

#### 5.4.6. Saline habitats

Saline habitats are reconstructed based on the presence of halophilic and halobiont species in the sediments, which constitute 8–12% in the samples S1–S6. Outside the sea coasts, halophilic species are good indicators of an arid climate, although many are hygrophilous, confined to the shores of permanent or temporary lakes: *Pogonus punctulatus* (Carabidae) or *Centorus* spp. (Tenebrionidae). Among Curculionidae, the xerophilic species *Sibinia staticis* (Becker, 1864) and *Anthypurinus basicornis* (Schultze, 1898) is associated with halobiont plants (Table 4; Dedyukhin and Korotyaev, 2021). The sample S7 revealed fragments of the only halophilic species *Bembidion aeneum* Germar, 1823 (Figs. 4, 3). This species is sometimes found on the shore of inland fresh water bodies (Lindroth, 1992b; Neri and Gudenzi, 2013) and therefore fossil remains of *B. aeneum* are not a sufficient basis for reconstruction of arid conditions.

#### 5.5. Extant distribution of species

Since the distribution of species largely reflects climatic and landscape-geographical conditions, a comparison of the recent and palaeodistributions allows us to draw conclusions about changes in environmental conditions. One of the characteristics is the proportion of buried species that currently inhabit the region.

As can be seen from the diagram (Fig. 6D), the smallest values of this indicator (24–27%) were found in samples S5 and S6, slightly more (32–40%) in samples S1, S2 and S4, while in samples S7, P1 and P2 it was even higher and shown 83–90% of species that inhabit the surrounding territories. The remaining species are not typical of the study region at the present time, i.e. their distributions are displaced in any direction(s). For the species from samples S1–S6, three main directions can be traced. Two of them (northern and southern) correspond to latitudinal zonation, and the third (eastern) can correlate with the continental climate.

The northern group (Supplementary Table 2) includes boreal and arcto-boreal species, which are distributed on the plain to the north of

the Gornovo site, i.e. they are recorded in the forest and/or tundra latitudinal zones, for example, *Otiorhynchus arcticus* (Fabricius, 1780) (Zinovyev et al., 2016). Most of the species from the northern group have boreomontane ranges, and in addition to the northern territories they are distributed in the mountains where are confined to high elevations. In total, 26 “northern” species were noted in samples S1–S6, and in each of the samples they make up 22–27% (Fig. 6D). Their presence in sediments unambiguously indicates colder conditions in the past. Samples P1 and P2 contain only one boreomontane species, the ground beetle *Pterostichus dilutipes*, while sample S7 does not contain the “northern” group at all.

Species distributed south of the site are characteristic of the steppe and semidesert zones of Eastern Europe, West Siberia and Kazakhstan (Fig. 7), or they have wider ranges and are distributed in the west to the Atlantic and in the east to the Far East. Some species of the “southern” group, in the west or east of the range, can be distributed significantly north of the Gornovo site. For example, the halophilic species *Bembidion aeneum* is distributed along the sea coasts up to 67°N (Lindroth, 1992b) and *Chrysolina purpurata* (Faldermann, 1833) is known in the lower reaches of the Indigirka River from latitude 65°N (Nogovitsyna, 2014). In the samples S1–S6, 30 species of Coleoptera were noted, the ranges of which are displaced to the south. They form from 25 to 27% (samples S2, S4, S6) to 34–39% (samples S1, S5) of the species. The combination of “southern” and “northern” species in one sample demonstrates that conditions were noticeably colder and drier than recent ones. In the samples S7, P1 and P2, southern species are not represented (an exception is the halophilic species *B. aeneum*).

The eastern group (Supplementary Table 2) includes the species whose range covers the territories to the east of the Gornovo site. Some of them have small ranges: Kazakh Upland and Western Altai (*Otiorhynchus bardus*; Legalov et al., 2016) or Altai-Sayan mountain system (*Pseudaplemonus martjanovi* and *Otiorhynchus janovskii*; Fig. 8; Gurina et al., 2019b). Others are widespread from the Altai-Sayan mountain system to North-Eastern Yakutia such as silphid *Aclypea altaica* (Gebler, 1830) (Averensky, 1999), or have a wider distribution in the Eastern

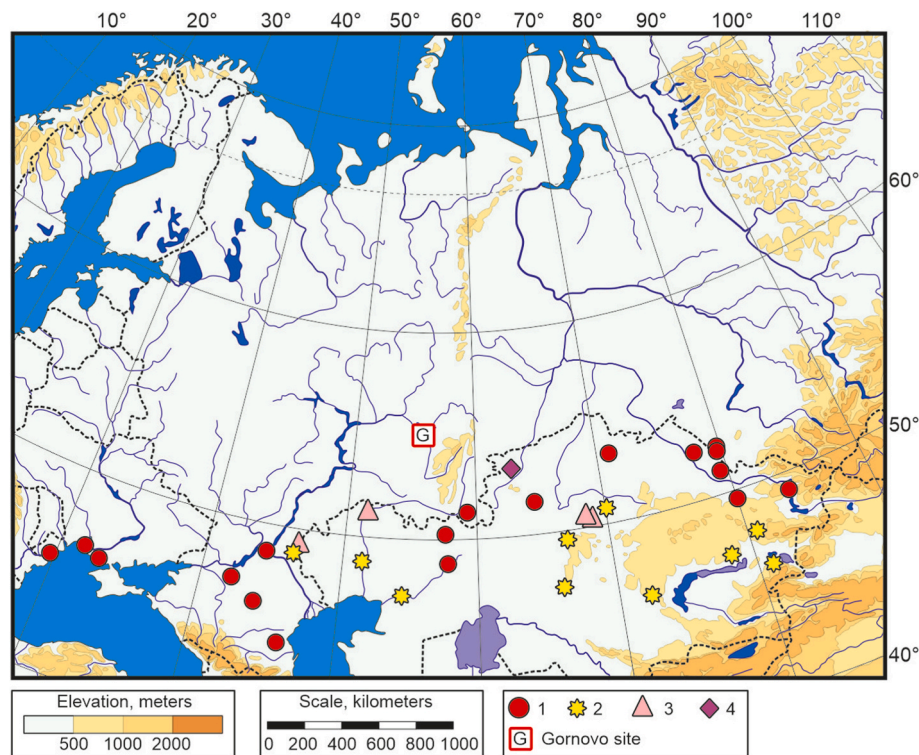


Fig. 7. Modern ranges of some Coleoptera from Gornovo IV deposits. 1 – *Anatolica abbreviata* (Tenebrionidae), 2 – *Aclypea bicarinata* (Silphidae), 3 – *Cymindis kasakh*, 4 – *Cribramara skopini* (Carabidae).





Fig. 8. Modern ranges of *Pseudaplemonus martjanovi* (Brentidae) and *Anthypurinus basicornis* (Curculionidae) from Gornovo IV deposits.

Palearctic and Western Nearctic such as the ground beetle *Harpalus amputatus* (Say, 1830) (Kataev, 1987). 12 eastern species were found in the site, where they account for 10–23% in the samples S1–S6 and are absent in the samples S7, P1 and P2 (Fig. 6D). The presence of “eastern” species in the sediments may be due to the greater continentality of the climate during the Late Pleistocene.

The western ranges are not typical for the species from the Gornovo site. Only *Notiophilus aestuans* Dejean, 1826 (Carabidae) is widespread in the Western Palearctic and barely reaches the Urals (Voronin and Esyunin, 2005).

Thus, the combination in the samples S1–S6 of species with northern and southern areas, as well as the presence of species from extracontinental regions of East Siberia, indicate cold and dry conditions at the time of formation of these deposits. On the contrary, Coleoptera assemblages from the samples S7, P1 and P2 are characteristic of the recent fauna of the study region, which indicates much milder humid climate. The presence of a boreal species suggests a somewhat colder climate than the recent one.

#### 5.6. Similar composition and similar age entomocomplexes of West Siberia

Comparison of entomocomplexes from samples S1–S6 revealed their very strong similarity to each other. These entomocomplexes are quite close to the periglacial entomofauna (stages MIS 3 and MIS 2) in the south of the West Siberian Plain. Due to the lack of dating in samples S1, S2, S4, S6 and the low accuracy of the radiocarbon date  $31455 \pm 1000$  BP for sample S5, it is not possible to attribute these to synchronous events reflected in the fluctuations of the entomofauna of this time on the current material. It can only be noted that entomocomplexes close to sample S5 by radiocarbon dates have also been described for the southern part of West Siberia. The first entomocomplex described in the region from sediments on the Tura River near the Malkovo village also gives a  $^{14}\text{C}$  date of  $31800 \pm 350$  BP (Kiselev, 1973; Zinovyev, 2011). In West Siberia, periglacial faunas are relatively well studied (Zinovyev, 2011; Gurina et al., 2019a). Although they differ sharply from the recent fauna of the West Siberian Plain, they share some common features with the faunas of the continental regions of the South Siberian mountains,

such as the Southeast Altai. Weevils of the genus *Otiorhynchus*, especially *O. bardus* and *O. af. ursus* usually predominate in periglacial entomocomplexes by the number of individuals. In terms of ecological preferences, entomocomplexes include both steppe and tundra species. The forest group is scarce or absent. The presence of halophilic species is very characteristic. Finally, most of the species from the sediments are absent in the recent fauna of the site, but according to their distribution patterns, the northern group of arcto-boreal and boreal species, the southern sub-boreal group, and the eastern group of species characteristic of sharply continental regions of Siberia can be distinguished. At the same time, a tendency towards a decrease in the proportion of arcto-boreal species from northern (ca.  $57^\circ\text{N}$ ) to southern (ca.  $51^\circ\text{N}$ ) sites is noticeable (Gurina et al., 2019a). In all these features, insect assemblages from samples S1–S6 are also undoubtedly form a single fauna. At the same time, Gornovo is not only the westernmost known site, but also the only one located west of the Ural Range. Also, one can distinguish regional features of the Gornovo insect assemblages. In comparison with the West Siberian ones they contain significantly more southern elements attributed to the steppe.

Entomocomplexes from the samples S7, P1 and P2, attributed to the end of stage MIS 3 as shown above, cannot be classified as periglacial steppe faunas, since they have a fundamentally different composition of beetles. A characteristic feature of these complexes is the absence of xerophilous and the predominance of intrazonal species that are characteristic of the region at the present time. A number of radiocarbon dates were obtained for sediments corresponding to the samples P1 and P2 (Supplementary Table 3). Five localities of insects from the territory of the West Siberian Plain from  $58$  to  $51.5^\circ\text{N}$  have close dates (Supplementary Table 3). Entomocomplexes fully corresponding to periglacial faunas have been described from the localities of Skorodum, Nizhnyaya Tavda, Nikitino and Shurala, all located between  $57$  and  $58^\circ\text{N}$  (Zinovyev, 2011). They include arctoboreal and steppe species (Zinovyev, 2011; Legalov et al., 2016). Humid forest and meadow species in these localities are represented singly, as in other periglacial faunas. The entomocomplex from the southernmost locality of this age, Kizikha-2 ( $51.5^\circ\text{N}$ ), includes a noticeably larger proportion of meadow species, which may indicate relatively humid conditions. At the same time, the presence of boreal species, along with the “southern” and

“eastern” steppe species, as well as halophilic species, makes it possible to consider the entomocomplex Kizikha-2 as part of the periglacial fauna of the region. Their moderate humid conditions may be associated with the relative location of these sites in the foothills of the Western Altai (Gurina et al., 2019a).

Thus, insects from the samples S1–S6 are similar to the Late Pleistocene entomocomplexes in the south of the West Siberian Plain (MIS 2 and MIS 3) and correspond to the periglacial steppe fauna. On the contrary, the insect composition of the samples S7, P1 and P2 does not correspond to entomocomplexes of the West Siberian Plain, which are close in age. This difference can be explained by the regional features of the Southern Urals foreland.

### 5.7. Temperature reconstructions using mutual climatic range method

MCR is a method for determining quantitative climatic indicators of the past, based on climate parameters in sites of recent distribution of species from sediments. This method was not only tested on insects, in particular Coleoptera, but also successfully used for climate reconstruction in Europe (Coope, 1977; Atkinson et al., 1986; Buckland et al., 2019), Northeast Siberia (Alfimov et al., 2003; Alfimov and Berman, 2009), Alaska (Elias et al., 1999; Elias, 2000, 2001), Japan (Shiyake, 2014) and other regions. Although the average temperature of the warmest month is usually reconstructed with high accuracy and is in good agreement with other data, problems arise with the reconstructions of winter temperatures (Elias, 1997; Alfimov et al., 2003; Buckland et al., 2019; Fletcher et al., 2019).

When using Coleoptera in the MCR, the question of the choice of the analysed species is also controversial. The developers of the method and some followers include only predatory beetles and saprophagous beetles in the analysis, while phytophagous beetles are excluded from consideration (Atkinson et al., 1986; Elias, 2000; Buckland et al., 2019). This choice is explained by the desire to avoid problems associated with delayed dispersal of host plants. This approach seems to be justified when reconstructing the conditions of the Pleistocene–Holocene transition, when conditions changed repeatedly over a short time, and radiocarbon dating allows us to accurately establish the chronology of these changes. It is also quite reasonable to exclude phytophagous beetles in the northern and humid regions from the analysis, where predators (Carabidae and Staphylinidae) predominate in numbers and species diversity. To determine the temperature parameters of the period of existence of periglacial steppes, when the conditions were relatively stable, and phytophagous species, especially in the southern regions, were abundant in zonal landscapes, it would be a mistake to exclude them from consideration. Thus, it was shown that even in the northern tundra-steppe of the lower reaches of the Kolyma River, phytophagous species were the most informative for establishing MCR (Alfimov and Berman, 2009).

The third problem, which limits the possibilities of using the MCR, is the small number of meteorological stations in Siberia. This is especially true in mountainous regions, where climatic parameters strongly depend on the altitude and topography of the area, and extrapolation of data can lead to a significant systematic error. For this reason, it was previously impossible to estimate the MCR for the periglacial faunas of the south of the West Siberian Plain. The recent distribution of most species from the sediments are confined to the mountains of South Siberia (Zinovyev et al., 2016).

As shown above, many Coleoptera species from the deposits of the Gornovo site have “southern” distribution ranges (Fig. 7), some of which are limited in distribution to plains. For these species, both predators and phytophagous, limits of  $T_{max}$  were identified, while we decided not to take into account winter temperatures. The most cryophilic species from the Gornovo site have extensive ranges, which is typical of Pleistocene sediments of various regions. Such species were used to identify MCRs in Europe and North America (Buckland, 2014; Elias, 2000).

#### 5.7.1. MCR of the humid assemblages

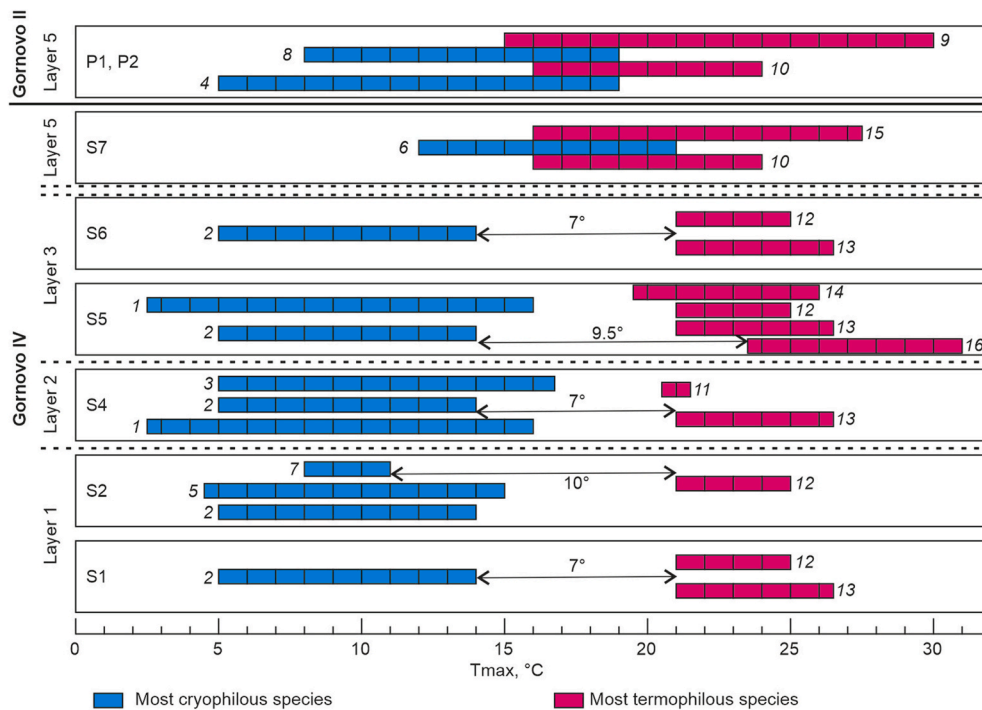
The diagrams (Fig. 9) show the  $T_{max}$  limits for the most cryophilic and most thermophilic species identified in each of the samples. In the samples P1 and P2, the most cryophilic species is *Pterostichus dilutipes*. Its southernmost distribution records on the plain are known from the Bolotnitsky District of the Novosibirsk Region (Trilikauskas and Dudko, 2016). At this point, the  $T_{max}$  is about +19 °C. A similar range, with the upper limit  $T_{max}$  +19 °C, is also given for *Patrobus septentrionis* (Elias, 2000). According to the BugsCEP database (Buckland, 2014), the most thermophilic species of these samples, *Platynus livens*, has a lower limit of  $T_{max}$  +16 °C. Thus, according to entomocomplexes from the samples P1 and P2, the average July temperatures are reconstructed from +16 to +19 °C, which is 1–4° colder than recent ones. Species from the sample S7 have a similar MCR from +16 to +21 °C (Fig. 9).

#### 5.7.2. Problems with MCR of periglacial assemblages

Fundamentally different shapes of the diagrams were revealed for species from the samples S1–S6 forming steppe periglacial entomocomplexes. The most cryophilic species in each of the samples have a significantly lower upper  $T_{max}$  limit than the lower limit of this indicator in thermophilic species, with the gap for the most contrasting species being 7–10 °C (Fig. 9). In other words, according to their modern distribution, the species from these samples do not have a common climatic range, and they cannot live together! Nevertheless, in all five samples with periglacial entomocomplexes, “incompatible” species were found to occur together, and most of the samples contain several thermophilic and several cryophilic species for which MCR is absent. In addition to those shown in the figure (Fig. 9),  $T_{max}$  <16 °C in all known sites for cryophilic species *Berninelsonius hyperboreus* (Elateridae), *Otiorynchus arcticus* (Curculionidae) and, probably, also *Pterostichus* (*Cryobius*) spp. (Carabidae). Similarly,  $T_{max}$  > 20 °C was found for the thermophilic *Sibinia staticis* (Curculionidae).

Single species that appear as exceptions have also been noted in other works using the MCR. They were excluded from consideration (Alfimov et al., 2003). The presence of such “deviating” species may be associated with an erroneous determination of subfossil material, redeposition or ingress of recent material during sampling, poor knowledge of the distributions, and an error in determining climatic parameters. In the case of the Gornovo entomocomplexes, redeposition seems unlikely to explain the pattern, if only because “incompatible” species were found in sediments of various ages. The explanation of ingress of recent material is untenable, since all the species mentioned here are absent from the fauna of the region. Errors in determining the palaeomaterial, of course, cannot be excluded. However, the presence of two series, cryophilic and thermophilic, with eight species each, with similar  $T_{max}$  values, allow us to have confidence in the result of cohabitation, even in the case of incorrect identification of individual representatives. Finally, the refinement of the data on the current distributions and on the average temperatures in the habitats will undoubtedly lead to some correction of the deduced  $T_{max}$  ranges. This is especially true for such little-known species as *Cribramara skopini* and *Cymindis kasakh*. The temperature range of *Pterostichus kokeilii*, listed in the BugsCEP database for the nominative subspecies, does not take into account closely related taxa from the eastern part of the range, *P. k. archangelicus* Poppius, 1907 and *P. tundrae* (Tschitscherine, 1894). Therefore, most likely, the size of the gap in the temperature range according to the current data may be somewhat overestimated. However, the upper limit of  $T_{max}$  15–16 °C for cryophilic species and the lower limit of  $T_{max}$  20–21 °C for thermophilic species are corroborated by several species (Fig. 9).

The combination of “incompatible” cryo- and thermophilic species in one complex means that they lived together in the past. Consequently, either cryophilic species could live at higher average July air temperatures, or thermophilic at lower temperatures, or the temperature preferences were different from the recent ones in both groups. In any case, some species from the periglacial entomocomplex currently do not



**Fig. 9.**  $T_{max}$  range for the most cryophilous (1–8) and most thermophilous (9–16) species from different samples of Gornovo II and Gornovo IV. 1 – *Diacheila polita*, 2 – *Bembidion dauricum*, 3 – *B. hastii*, 4 – *Patrobus septentrionis*, 5 – *Pterostichus brevicornis*, 6 – *P. mannerheimii*, 7 – *P. kokeilii*, 8 – *P. dilutipes* (Carabidae); 9 – *Agonum versutum*, 10 – *Platynus livens*, 11 – *Cribramara skopini*, 12 – *Cymindis kasakh* (Carabidae), 13 – *Aclypea bicarinata* (Silphidae), 14 – *Anatolica abbreviata* (Tenebrionidae), 15 – *Thryogenes festucae*, 16 – *Anthypurinus basicornis* (Curculionidae).

realize their full “temperature potential”. This does not necessarily imply a change in the thermal preferendum of these species.

The  $T_{max}$  is one of the indicators of the macroclimate, which indirectly affects the microclimatic conditions, such as the temperature of the soil in the habitats of each species. Suitable microclimatic conditions, which limit the distribution of species, can be realized only under certain parameters of the macroclimate (including  $T_{max}$ ). It is likely that during the existence of periglacial steppe landscapes in the study region, microclimatic conditions were suitable for both cryo- and thermophilic species, i.e. there was a sharp contrast between the summer temperatures of the soil in the warmest and coldest biotopes. Such a contrast could only be achieved in an extracontinental climate. It is known that an increase in continentality affects, first of all, the driest, most heated areas of the surface, which become even more heat-supplied. In this case, the limiting factor for thermophilic species is not average temperatures, but the sum of positive temperatures in the upper soil layers (Berman and Alfimov, 1993, 1998). Consequently, optimal conditions for thermophilic species are achieved in a continental climate at low average temperatures in July, and the greater the continentality, the lower the  $T_{max}$  is required for the existence of the species. The coldest soils under the moss-lichen cover, located on the permafrost close to the surface, have the pattern of low temperature being almost independent of continentality (Alfimov et al., 2003). Therefore,  $T_{max}$  for cryophilic species depends on continentality to a lesser extent.

At present, the conditions closest to periglacial are being realized in the mountains of Southern Siberia and Northern Mongolia, especially in the Southeastern Altai (Chytrý et al., 2019; Gurina et al., 2019a). In particular, many species from the Gornovo site, both cryophilic and relatively thermophilic, range this region. For example, *Aclypea sericea* lives in the “warmest” part of the region – in the center of the Chuya Depression with an absolute altitude of 1800 m above sea level, where  $T_{max}$  is about +14 °C. Some of the most cryophilic species (*Diacheila polita*, *Pterostichus brevicornis*), on the contrary, are found only on the Ukok Plateau or in the belt of mountain tundra with absolute heights of 2400 m above sea level and higher (Dudko et al., 2010). It turns out that even in the Southeastern Altai, a mountainous region with an extracontinental climate with the mosaic landscapes due to many factors including macro relief, not all cryo- and thermophilic species can occur

together. Under conditions of formation of sediments of the samples S1–S6 in Gornovo, these species lived together on a plain territory, and the contrast of temperatures in habitats here was realized only with the participation of meso- and micro-relief. It follows from this that the continentality of the climate during the existence of periglacial landscapes on the East European Plain was significantly higher than now in the regions that are closest in climatic conditions.

Thus, dependence of steppe thermophilic species on the heat supply of habitats, which can be achieved at different values of  $T_{max}$ , depending on continentality, greatly complicates the use of these species for reconstructing macroclimate parameters. This circumstance is aggravated by the fact that recent steppe landscapes are largely fragmented and the ranges of many steppe species are more or less disjunctive. At the same time, based on the distribution, it is impossible to understand whether the reason for the absence of a species in a particular region relates to recent climatic parameters or to historical factors. These difficulties are clearly seen from the analysis of the distribution of two species of carrion beetles *Aclypea sericea* and *A. bicarinata*. Both species are regularly found in the Late Pleistocene sediments of the south of Western Siberia (Zinoviyev, 2011; Tsepelev et al., 2013) and are quite abundant in the samples S1–S6 (Table 3). Their almost coinciding recent ranges cover the steppe zone within the southeast of European Russia and Central Kazakhstan, while *A. sericea* also has an isolated locality – the Chuya Depression of Southeastern Altai (Fig. 7; Nikolajev, 2010; Tsepelev et al., 2013). The average July temperature of the plain part of the range of these species does not exceed 21 °C, and in the Chuya depression it is about 14 °C. It is likely that under the conditions of an even more continental climate of periglacial landscapes, these species could live even at lower  $T_{max}$  values; therefore, the lower estimate for the total temperature range obtained from the recent distribution of species is incorrect. Other similar examples of disjunctive distribution of steppe beetle species are considered in Zinoviyev (2006). Cryophilic species probably give an acceptable estimate of summer air temperatures, and the presence of the most cold-loving species in the sediment can be used for an estimate of an upper value of  $T_{max}$ .

Thus, the MCR method for determining the average July air temperature based on Coleoptera is correct to use for landscapes or natural zones close to recent ones. The use of this method for periglacial (tundra-



steppe) landscapes is very problematic, since recent species ranges do not allow revealing the actual lower limits of the habitat of thermophilic species. The obtained temperature estimates can be overestimated.

Nevertheless, even the upper limit of  $T_{max}$  can be very informative for reconstructions. Thus, entomocomplexes from the samples S1–S6 have, in general, a rather southern appearance with a predominance of species common in the steppe zone. However, the reconstructed  $T_{max}$  lower than +15 °C shows that these deposits belong to relatively cold stages, and the predominance of thermophilic species is associated with the contrast of microconditions and the wide distribution of well-heated biotopes. The dated sample S5 from Gornovo IV (34723–36809 cal BP) is also attributed to this assemblage, which can be compared with the second cooling of MIS 3 (Laukhin et al., 2015). On the contrary, humid entomocomplexes from the samples S7, P1 and P2 (ca. 31500 cal BP), which have a slightly more northerly appearance than the recent one, are compared with the third (last) warming of MIS 3. Reconstructed temperatures from +16 to +19 °C correspond to this interpretation.

### 5.8. Summarizing mollusc analysis of palaeoenvironments

The composition of molluscs and their ecological preferences indicate a river valley that existed during the accumulation of the lower part of the terrace (Gornovo III, layer 4; Gornovo II, layer 6). On the floodplain, there were water bodies that connected with the river during the flooding, as indicated by the finds of the shells *Sphaerium rivicola*, *S. corneum*, *Pisidium amnicum*, *P. supinum*, which prefer the muddy bottom of rivers with slowly flowing waters. The interlayering of sands with cross-bedding and clays confirms the temporary connection of stagnant shallow water bodies with the river bed during floods. Rare vegetation, among which a few terrestrial molluscs lived, grew on the banks of a river.

A complex of molluscs, consisting of freshwater and terrestrial species was found from the clays up section. The mollusc species composition helped to reconstruct a stagnant water body (an oxbow) separated from the river (Gornovo IV, layer 5). The existence of an oxbow is confirmed by the absence of Spheriidae bivalves, as well as by the abundance of gastropods (*Lymnaea*, *Anisus*, *Planorbis*, *Gyraulus* and *Valvata*). These gastropods live in the coastal part of the oxbows with slow-flowing or stagnant waters, with a silted and well-warmed bottom and rich aquatic vegetation.

Gradually, the oxbow was overgrown (Gornovo II, layers 2 and 3; Gornovo I, layer 7); it was inhabited by numerous freshwater gastropods. The herbaceous plants grew on its banks and served as food for terrestrial molluscs. Also, there were shrubs and trees, which are indicated by a typical forest species *Discus ruderatus*. Despite the fact that the species composition of terrestrial molluscs practically was the same, their number has increased suggesting a favourable environment with moderate temperatures.

During the accumulation of dense loam (Gornovo I, layers 6 and 5; Gornovo II, layer 1), a sharp change in climate occurred, as evidenced by the scarce finds of molluscs (compared to the underlying sediments). Rare *Lymnaea palustris* and *Anisus spirorbis* inhabited the water body. Terrestrial molluscs were transported to the water from the slopes. The presence of *Dreissena polymorpha* suggests the redeposition from the Lower Pleistocene deposits.

The presence of a few shells of terrestrial molluscs in the loess-like loam (Gornovo I, layer 2) indicates their accumulation under subaerial conditions. The presence of brackish-water *Pyrgula* cf. *trivialis* and *Clessiniola* sp. in these deposits testifies to their short-range transport from the Lower Pleistocene localities near the site.

## 6. Conclusion

Results of the study demonstrated that the first above floodplain terrace of the Belaya River near the Gornovo village is constituted by the Upper Pleistocene sediments. These are sands and clays with remnants

of insects and plants of the middle of the Tabulda time with a sharply continental climate (MIS 3); oxbow clay with the mammals bone artefacts, insects, and molluscs that lived in a temperate climate (MIS 3); dense loam with rare organic remains presumably corresponding to the time of maximum cooling, or the beginning of the Kudashevo time (Last Glacial Maximum, MIS 2); loess-like loam accumulated in the periglacial environment that is the second half of the Kudashevo time (Late Glacial, MIS 2), and the soil completing the section, is the undivided Holocene (MIS 1).

The malacofauna of Gornovo I–IV includes 27 species of terrestrial and freshwater molluscs. Their shells are numerous and diverse in the MIS 3 sediments, but, on the contrary, poorly represented by singletons in MIS 2. This indicates a significant deterioration of climatic conditions between the stages. Qualitative and quantitative changes in the composition of molluscs during MIS 3 reflect successive changes in the reservoir at the Gornovo site. The sediments of the lower layers correspond to a reservoir that periodically was connecting to the river; the clays of the middle layers of MIS 3 are represented by stagnatophilic species, according to which a stagnant reservoir is reconstructed; and the complex of molluscs corresponds to an overgrown oxbow described from the upper part of the Tabulda horizon.

New materials on insects from the Gornovo site are the only known Quaternary insect locality in the Southern Urals foreland. Most of the species belong to the order Coleoptera, represented by 17 families and 142 species.

Coleoptera assemblages from the layers attributed to the middle of MIS 3 correspond to the periglacial type of faunas that have no close contemporary analogues. Faunas of this type are known only for Late Pleistocene deposits of age MIS 3 and MIS 2 in the southern part of the West Siberian Plain. The periglacial entomocomplexes of Gornovo, like the West Siberian ones, are characterized by the predominance of Curculionidae and Carabidae species, and in terms of the number of individuals, by the dominance of *Otiorhynchus bardus* and *O. af. ursus*. The group of steppe species is most represented, but tundra, forest, meadow, near-water and halophilic species are also noted in all complexes. Most of the species from the Gornovo entomocomplexes are absent in the recent regional fauna and are distributed to the north, south, or east of this site. A distinctive feature of the periglacial entomocomplexes of Gornovo, in comparison with the West Siberian ones, is a large proportion of steppe species.

Coleoptera assemblages from the layers attributed to the end of MIS 3 differ sharply from the preceding ones and are attributed to the boreal humid faunas. The majority of species belonging to the Carabidae, while Curculionidae there are represented much poorer. All samples contain *Platynus livens*, which can be considered as a precise marker of humid-adapted entomocomplexes. The complex contains the sharply predominant near-water and forest ecological groups. The humid entomocomplexes of Gornovo show little resemblance to entomofaunas of similar age in the south of the West Siberian Plain. Most of the species inhabit the region at the present time.

The Mutual Climatic Range method was used to reconstruct the mean July air temperatures ( $T_{max}$ ) from entomological data for the boreal humid entomocomplexes and for cryophilic species of Coleoptera periglacial entomocomplexes. Thermophilic (steppe) species from the periglacial complexes cannot be used for  $T_{max}$  reconstructions, since they live at higher air temperatures under recent conditions than they could live in the extracontinental climate of the Pleistocene.

According to the data of entomological analysis, dry and cold conditions of the extracontinental climate are reconstructed in the middle of MIS 3 of the Southern Fore-Urals ( $T_{max}$  was not higher than +15 °C). In the region, open tundra-steppe landscapes with the presence of coniferous forests are reconstructed. Forb steppe probably prevailed, while forest and meadow areas were confined to river floodplains. Tundra or tundra-like habitats were formed in the least warmed areas of the relief under very moist conditions, which could be provided by permafrost close to the surface. This time was probably favourable for many large



mammals, as evidenced by both direct finds of bones and entomological data. A slight warming of the climate at the end of MIS 3 led to a significant softening of climatic conditions ( $T_{max} = 16\text{--}19\text{ }^{\circ}\text{C}$ ) and a dramatic restructuring of landscapes. Humid conditions, as well as meadow and forest landscapes are reconstructed based on entomological complexes. It is likely that the humidification of this period was of a regional nature and was due to the proximity to the Southern Urals mountains.

### Author contributions

The original draft was completed by R.D. and all co-authors. R.D. and G.D. designed the study. R.D. suggested ideas for discussion and prepared figures. The stratigraphical analysis was conducted by G.D. and E.O.; the insect fauna was studied by R.D., E.Z. and A.G. (Coleoptera), A.I. (Histeridae, Scarabaeidae, Tenebrionidae), Y.M. (Chrysomelidae), A.P. (Elateridae), A.S. (Staphylinidae), A.L. (Brentidae, Curculionidae, Scolytidae); the molluscs were studied by E.O. and G.D. All authors contributed to the writing, discussion, reviewing, and editing of the manuscript.

### Data availability

The collections of insects are kept at the Institute of Systematics and Ecology of Animals, Siberian Branch of the RAS (Novosibirsk, Russia). The collections of molluscs N 012 (Gornovo I), N 044 (Gornovo II), N 275 (Gornovo III) and N 384 (Gornovo IV) are kept at the Institute of Geology UFRS RAS (Ufa, Russia).

### Declaration of competing interest

There is no conflict of interests in our manuscript.

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### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.quaint.2021.10.003>.

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